A Scientific Review of the Potential Environmental Effects of Aquaculture in Aquatic Ecosystems

Volume V

Behavioural Interactions Between Farm and Wild Salmon: Potential for Effects on Wild Populations
(Laura K. Weir and Ian A. Fleming)
Overview of the Environmental Impacts of Canadian Freshwater Aquaculture
(C.L. Podemski and P.J. Blanchfield)
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TABLE OF CONTENTS

Editorial Board vi
Foreword vii
Avant-Propos ix

Behavioural Interactions Between Farm and Wild Salmon: Potential for Effects on Wild Populations
(Laura K. Weir and Ian A. Fleming)

Executive Summary 1
    Knowledge Gaps 2
Sommaire 3
    Lacunes dans les connaissances 4
Introduction 6
Background 6
Dispersion and migratory behaviour of escaped fish 7
    Dispersion following escape 7
    Survival and feeding performance following escape 8
    Homing and straying to rivers 10
    Within river migratory patterns 11
    Conclusions 12
Breeding performance, behaviour and interactions 13
    Femal spawning characteristics 13
    Male spawning characteristics 14
    Age at maturity 15
    Survivorship during and following breeding 15
    Maternal effects on offspring 16
    Conclusions 16
Offspring survival and perfomance 17
    Diet/foraging/habitat selection 17
    Growth Rate 18
    Aggression/dominance 19
    Predator avoidance 20
    Conclusions 20
References 22

Overview of the Environmental Impacts of Canadian Freshwater Aquaculture
(C.L. Podemski and P.J. Blanchfield)

Executive summary 30
    Knowledge gaps and research priorities 33
Sommaire 35
    Lacunes dans les connaissances et priorités de la recherche 38

Introduction 40
Waste production 42
Solid wastes 43
Dissolved wastes 45
Effects of wastes 46
    Dissolved oxygen concentrations 46
    Changes in water nutrient concentrations 49
    Microbial communities 51
    Phytoplankton communities 52
    Zooplankton communities 54
Benthic effects 54
    Sediment characteristics 54
    Effects on zoobenthos 55
    Benthis recovery 59
Fish populations 59
Trophic effects 60
Native-farmed fish interactions 61
    Effects on native fish communities 62
    Genetic interactions 64
Knowledge gaps and research needs 65
Acknowledgments 68
References 69

A Scientific Review of Bivalve Aquaculture: Interaction Between Wild and Cultured Species
(T. Landry, M. Skinner, A. LeBlanc, D. Bourque, C. McKindsey, R. Tremblay, P. Archambault, L. Comeau, S. Courtenay, F. Hartog, M. Ouellette and J.M Sevigny)

Executive summary 80
Sommaire 83
Introduction 87
Pelagic community and bivalve culture interactions 88
    Knowledge gaps and recommended research 90
Benthic community and bivalve aquaculture interactions 90
    Biodepositionn and sedimentation 91
    Assemblage change 92
    Hydrodynamic influence 95
    Far-field interactions 95
    Physical alterations 96
        Substrate enhancement 96
        Predator removal 96
        Maintenance and harvesting activities 97
    Epibionts 98
    Knowledge gaps and recommended research 99
Predator effects related to bivalve culture 100

  Knowledge gaps and recommended research 101
Exotic species related to bivalve aquaculture 102
  History of exotic bivalve introductions for aquaculture and their role as vectors for other exotics 103
  Exotic bivalves as habitat, competition with endemic species, and ecosystem effects 104
  Exotic hitchhikers 106
  Exotic macrospecies 106
  Exotic toxic and nuisance phytoplankton 108
  Exotic parasites and diseases 110
  Management issues 110
    Risk assessment 110
    Caveats with respect to spread and predictions of ecological effects 112
    Quarantine, disinfection and other protocols to limit risk 113
  Knowledge gaps and recommended research 115
Genetic interactions between cultured and wild bivalve 115
  Risks associated with culture conditions 116
  Risks associated with transfers of organisms 117
  Knowledge gaps and research recommendations 118
Acknowledgements 119
References 120

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FOREWORD

Context

The Government of Canada is committed to ensuring the responsible and sustainable development of the aquaculture industry in Canada. The Minister of Fisheries and Oceans' announcement of the $75 M Program for Sustainable Aquaculture (PSA), in August 2000, is a clear expression of this commitment. The objective of the PSA is to support the sustainable development of the aquaculture sector, with a focus on enhancing public confidence in the sector and on improving the industry's global competitiveness. Ensuring the sector operates under environmentally sustainable conditions is a key federal role.

As the lead federal agency for aquaculture, Fisheries and Oceans Canada (DFO) is committed to well-informed and scientifically-based decisions pertaining to the aquaculture industry. DFO has an ongoing program of scientific research to improve its knowledge of the environmental effects of aquaculture. The department is also engaged with stakeholders, provinces and the industry in coordinating research and fostering partnerships. As a contribution to the Federal government's Program for Sustainable Aquaculture, DFO is conducting a scientific review of the potential environmental effects of aquaculture in marine and freshwater ecosystems.

Goal and Scope

Known as the State-of-Knowledge (SOK) Initiative, this scientific review provides the current status of scientific knowledge and recommends future research studies. The review covers marine finfish and shellfish, and freshwater finfish aquaculture. The review focuses primarily on scientific knowledge relevant to Canada. Scientific knowledge on potential environmental effects is addressed under three main themes: effects of wastes (including nutrient and organic matter); chemicals used by the industry (including pesticides, drugs and antifoulants); and interactions between farmed fish and wild species (including disease transfer, and genetic and ecological interactions).

This review presents potential environmental effects of aquaculture as reported in the scientific literature. The environmental effects of aquaculture activities are site-specific and are influenced by environmental conditions and production characteristics at each farm site. While the review summarizes available scientific knowledge, it does not constitute a site-specific assessment of aquaculture operations. In addition, the review does not cover the effects of the environment on aquaculture production.

The papers target a scientific and well-informed audience, particularly individuals and organizations involved in the management of research on the environmental interactions of aquaculture. The papers are aimed at supporting decision-making on research priorities, information sharing, and interacting with various organizations on research priorities and possible research partnerships.

Each paper was written by or under the direction of DFO scientists and was peer reviewed by five experts. The peer reviewers and DFO scientists help ensure that the papers are up-to-date at the time of publication. Recommendations on cost-effective, targeted research areas will be developed after publication of the full series of SOK review papers.

State-of-Knowledge Series

DFO plans to publish 12 review papers as part of the SOK Initiative, with each paper reviewing one aspect of the environmental effects of aquaculture. This Volume contains 3 papers: Behavioural Interactions Between Farm and Wild Salmon: Potential for Effects on Wild Populations; Overview of the Environmental Impacts of Canadian Freshwater Aquaculture; and A Scientific Review of Bivalve Aquaculture: Interaction Between Wild and Cultured Species.

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AVANT-PROPOS

Contexte

Le gouvernement du Canada est déterminé à assurer le développement responsable et durable de l'industrie aquacole au Canada. Le Programme d'aquaculture durable (PAD) de 75 millions de dollars annoncé par le ministre des Pêches et des Océans en août 2000 traduit clairement cet engagement. Ce programme vise à soutenir le développement durable du secteur aquacole, surtout en améliorant la confiance du public envers l'industrie et la compétitivité globale de celle-ci. Veiller à ce que l'industrie fonctionne dans des conditions durables sur le plan environnemental constitue une responsabilité essentielle du gouvernement fédéral. À titre d'organisme fédéral responsable de l'aquaculture, Pêches et Océans Canada (MPO) est déterminé à prendre des décisions éclairées qui reposent sur des données scientifiques éprouvées en ce qui concerne l'industrie aquacole. Le MPO mène un programme de recherches scientifiques pour améliorer ses connaissances sur les effets de l'aquaculture sur l'environnement. Le Ministère collabore également avec des intervenants, les provinces et l'industrie à la coordination des recherches et à l'établissement de partenariats. Le MPO contribue au Programme de l'aquaculture durable du gouvernement fédéral en passant en revue la littérature scientifique qui aborde les effets possibles de l'aquaculture sur les écosystèmes marins et d'eau douce.

Objectif et portée

Désignée projet sur l'état des connaissances, cette revue de la littérature définit l'état actuel des connaissances scientifiques sur les effets de l'élevage de poissons et de mollusques en mer et de la pisciculture en eau douce et fait des recommandations de recherches futures. La revue, qui se concentre surtout sur les connaissances scientifiques applicables au Canada, les aborde sous trois thèmes principaux : les impacts des déchets (éléments nutritifs et matière organique), les produits chimiques utilisés par l'industrie (pesticides, médicaments et agents antisalissures) et les interactions entre les poisons d'élevage et les espèces sauvages (transfert de maladies et interactions génétiques et écologiques).

Cette revue présente les effets environnementaux possibles de l'aquaculture documentés dans la littérature scientifique. Les effets environnementaux des activités aquacoles dépendent du site, des conditions environnementales et des caractéristiques de production de chaque établissement aquacole. L'examen résume les connaissances scientifiques disponibles mais ne constitue pas une évaluation des activités aquacoles spécifique au site. L'examen ne porte pas non plus sur les effets de l'environnement sur la production aquacole.

Les articles sont destinés à un auditoire de scientifiques et de personnes bien informées, notamment des personnes et des organisations participant à la gestion de la recherche sur les interactions environnementales de l'aquaculture. Les articles visent à soutenir la prise de décision sur les priorités de recherche, la mise en commun de l'information et les interactions entre diverses organisations concernant les priorités de recherche et les partenariats de recherche possibles.

Rédigées par des scientifiques du MPO ou sous leur supervision, les articles ont été contrôlés par des pairs, ce qui assure qu'ils sont à jour au moment de leur publication. Après la publication de toute la série d'articles sur l'état des connaissances, des recommandations de recherches ciblées et rentables seront faites.

Série sur l'état des connaissances

Dans le cadre du projet de l'état des connaissances, le MPO prévoit publier douze articles de synthèse portant chacun sur un aspect des effets environnementaux de l'aquaculture. Le présent volume contient les trois articles suivants : Interactions comportementales entre le saumon d'élevage et le saumon sauvage – effetc possibles sur les populations sauvages; Un aperçu général des impacts écologiques d'aquaculture d'eau douce en canada; et Examen scientifique de l'élevage de bivalves : interaction entre les espèces d'élevage et les espèces sauvages.

Renseignements supplémentaires

Pour de plus amples renseignements sur un article, veuillez communiquer avec son auteur principal. Pour de plus amples renseignements sur le projet de l'état des connaissances, veuillez communiquer avec :

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BEHAVIOURAL INTERACTIONS BETWEEN FARM AND WILD SALMON: POTENTIAL FOR EFFECTS ON WILD POPULATIONS

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EXECUTIVE SUMMARY

Behavioural interactions between farm and wild fish occur at all three stages mentioned in this review. The ability of farm fish to migrate into rivers following escape from aquaculture in the ocean environment leads to interactions during breeding. As not much is known about salmon during the marine phase of their life cycle, it is difficult to assess how interactions between farm and wild fish will ultimately affect wild populations at this stage. However, farm fish show aberrant migratory patterns, most notably that they may disperse into many rivers and thus may affect more than one wild population. The effects of behavioural interactions between farm and wild fish are most evident during breeding. Farm females and mature male parr represent the most likely means of gene flow from farm to wild populations, which are enhanced by earlier ages at maturity of farm fish because of faster growth rate. However, behavioural interactions on the spawning grounds by large males and females, as well as mature male parr, can negatively influence the reproductive success of wild fish. Pure farm and hybrid offspring in the freshwater environment can effectively compete for food and space with wild individuals, and at this life stage the environmental effects of aquaculture rearing are diminished. Maternal effects heavily influence the success of farm offspring at early juvenile stages, and their survival is usually poor compared to wild fish (e.g. Fleming et al. 2000, McGinnity et al. 2003). In addition, farm juveniles are sometimes less successful at evading predators and are not usually dominant over wild fish in natural environments.

While overall trends suggest that farm and hybrid fish may not behave similarly to wild fish, and indeed have lower survival (e.g., McGinnity et al. 2003), variation among studies reflects the context-dependent nature of determining whether farm fish are successful in the wild. Their effect will depend upon a number of factors, including genetic origin, rearing conditions, the number, timing, magnitude and frequency of escapes, and the state of the wild population (Hutchings 1991). Thus, risk assessment will need to focus on those factors mostly likely to generate exposure to the hazard (e.g. escape), and to influence the risk of harm given an escape and the severity of that harm (e.g., Kapuscinski 2005). It will also need to recognize and incorporate various types of uncertainty. A key outcome of this process should be risk reduction planning and implementation.

KNOWLEDGE GAPS

Despite the growing number of studies on the subject, there remain many areas where little is known about the potential effect of farm fish on wild populations. Our report focuses mainly on the trends among studies investigating differences between farm and wild fish. However, significant variation exists among studies, emphasizing that the outcome of interactions between farm and wild fish is likely context-dependent. Some studies show that the outcome of interactions, or the magnitude of differences, between farm and wild fish depends upon the farm strain and wild population under comparison (e.g. Einum and Fleming 1997, Weir et al. 2004). This may be due to a lack of understanding of the interaction between the genetic and environmental effects of aquaculture on farm fish. Elucidating the effects of genetics and environment is important to assess how farm fish of different origin may affect specific wild populations. While some studies indicate that genetic changes may be occurring in some wild populations following farm escape (e.g. Crozier 1993, 2000), there is no documented indication that escaped farm fish are directly causing demographic changes in wild populations, although strong inference can be drawn from two whole-river release experiments that indicate this is likely the case (Fleming et al. 2000, McGinnity et al. 2003). From the population demographic perspective, survival and competition at sea of both wild and farm fish is not well known. In addition, our knowledge of the migratory and straying behaviour of escaped farm fish remains rudimentary despite the fact that aquaculture fish are most likely to escape from sea pens and their first interactions with wild individuals is in the adult migratory phase. While there are substantive data regarding interactions between farm and wild fish in artificial or semi-natural environments, field data documenting farm-wild behavioural interactions in rivers are also lacking, most notably for juveniles. Furthermore, although lifetime fitness over one or more generations has been studied (Fleming et al. 2000, McGinnity et al. 2003), the long-term demographic consequences of decreased farm fish fitness relative to wild in the natural environment have yet to be determined. While significant strides have been made in the state of knowledge regarding farm-wild interactions to allow risk assessment, knowledge gaps remain by which associated uncertainty could be reduced. A formal investigation of knowledge gaps, that includes sensitivity analyses of population dynamic/gene flow models, is needed to determine the types of studies to be undertaken to decrease existing uncertainty.

INTERACTIONS COMPORTEMENTALES ENTRE LE SAUMON D'ÉLEVAGE ET LE SAUMON SAUVAGE – EFFETS POSSIBLES SUR LES POPULATIONS SAUVAGES

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SOMMAIRE

Il existe des interactions comportementales entre les poissons d'élevage et les poissons sauvages aux trois stades mentionnés dans le présent examen. La capacité qu'ont les saumons d'élevage à migrer vers des rivières après s'être évadés de sites piscicoles en milieu océanique donne lieu à des interactions avec les saumons sauvages durant la période de reproduction. Puisque nous en connaissons très peu sur le saumon lors de la partie de son cycle de vie passée en milieu marin, il est difficile d'évaluer quels seront les effets à long terme des interactions entre les saumons d'élevage et les saumons sauvages sur les populations sauvages au stade de reproduction. Cependant, les saumons d'élevage montrent des régimes de migration aberrants, notamment en raison du fait qu'ils peuvent se disperser dans de nombreuses rivières et ainsi avoir des conséquences pour plus d'une population sauvage. Les effets des interactions comportementales entre les saumons d'élevage et les saumons sauvages sont plus évidents lors de la période de reproduction. Les femelles et les tacons mâles matures d'élevage constituent les éléments les plus probables du flux génétique entre les populations d'élevage et les populations sauvages, l'importance de ces éléments étant accrue par le fait que les saumons d'élevage viennent à maturité en plus bas âge en raison d'une vitesse de croissance plus rapide. Cependant, les interactions comportementales sur les lieux de fraie avec les mâles et les femelles de grande taille, ainsi qu'avec les tacons mâles matures, peuvent avoir des effets néfastes sur le succès de reproduction des poissons sauvages. La progéniture d'élevage et hybride dans les milieux d'eau douce peuvent faire concurrence aux poissons sauvages pour la nourriture et le territoire. De plus, à ce stade, les effets de l'aquaculture sur l'environnement sont réduits. Les effets maternels ont une grande incidence sur le succès de la progéniture d'élevage aux premiers stades juvéniles, et la survie de celle-ci est habituellement faible par rapport à celle des poissons sauvages (Fleming et al., *2000; McGinnity* et al., *2003). En outre, les juvéniles d'élevage ont parfois plus de difficultés à échapper aux prédateurs et ne sont habituellement pas dominants par rapport aux poissons sauvages en milieu naturel.*

Tandis que les tendances générales suggèrent que les poissons d'élevage et les poissons hybrides pourraient ne pas avoir un comportement semblable aux poissons sauvages, ils ont en effet un taux de survie moins élevé (McGinnity et al., *2003), les différences entre les études illustrent que le succès des poissons d'élevage dans la nature ne peut être déterminé qu'en tenant compte du contexte. Les effets des poissons d'élevage dépendent d'un certain nombre de facteurs, y compris l'origine génétique, les conditions d'élevage,*

le nombre, le moment, l'importance et la fréquence des évasions, et l'état de la population sauvage (Hutchings, 1991). Ainsi, l'évaluation des risques devra porter sur les facteurs qui sont les plus susceptibles d'entraîner une exposition au danger (évasion) et de faire varier le niveau de risque et l'importance des dommages (Kapuscinski, 2005). Cette évaluation devra également tenir compte de divers types d'incertitude. Un résultat important de ce processus devrait être un plan de réduction des risques et la mise en œuvre de ce plan.

LACUNES DANS LES CONNAISSANCES

Malgré le nombre croissant d'études sur le sujet, il existe encore de nombreuses lacunes en ce qui concerne les effets possibles des poissons d'élevage sur les populations sauvages. Notre rapport porte principalement sur les tendances qui ressortent des études sur les différences entre les poissons d'élevage et les poissons sauvages. Il existe toutefois des différences importantes entre les résultats des diverses études, ce qui met en évidence le fait que les conséquences des interactions entre les poissons d'élevage et les poissons sauvages dépendent probablement du contexte. Certaines études montrent que les conséquences des interactions, ou l'ampleur des différences, entre les poissons d'élevage et les poissons sauvages varient en fonction de la souche d'élevage et de la population sauvage concernées (Einum et Fleming, 1997; Weir et al.*, 2004). Cela est peut-être attribuable à un manque de connaissances sur l'interaction entre les effets génétiques et environnementaux de l'aquaculture sur les poissons d'élevage. Il est important de connaître ces effets pour évaluer comment des poissons d'élevage d'origine différente peuvent avoir une incidence sur certaines populations sauvages. Certaines études indiquent que des changements génétiques peuvent se produire chez certaines populations sauvages à la suite de l'évasion de poissons d'élevage (Crozier 1993 et 2000), mais il n'existe aucun document prouvant que les poissons d'élevage évadés sont directement responsables de changements démographiques chez des populations sauvages. Il est toutefois possible de tirer des conclusions solides en ce sens en se fondant sur deux expériences de libération dans des rivières (Fleming* et al.*, 2000; McGinnity* et al.*, 2003). Du point de vue démographique, nous en connaissons peu sur la survie et la concurrence en mer des poissons d'élevage et des poissons sauvages. De plus, nos connaissances sur les comportements de migration et d'errance des poissons d'élevage évadés demeurent rudimentaires malgré le fait que les poissons d'élevage ont plus de chances de s'évader d'enclos en mer et que leurs premières interactions avec des poissons sauvages se produisent lors de la migration au stade adulte. Il existe des données de fond sur les interactions entre les poissons d'élevage et les poissons sauvages en milieux artificiels ou semi-naturels, mais il manque de données de terrain sur ce type d'interactions dans les rivières, notamment en ce qui concerne les juvéniles. De plus, bien que la valeur adaptative globale pendant une génération ou plus ait déjà été étudiée (Fleming* et al.*, 2000; McGinnity* et al.*, 2003), les conséquences démographiques à long terme d'une baisse de la valeur adaptative des poissons d'élevage par rapport à celle des poissons sauvages en milieu naturel n'ont toujours pas été déterminées. Des progrès importants ont été réalisés en ce qui a trait à l'approfondissement des connaissances sur les interactions entre les poissons d'élevage et les poissons sauvages afin de permettre* *une évaluation des risques, mais il reste encore des lacunes dans les connaissances qui constituent des sources d'incertitude. Une étude officielle de ces lacunes, qui comprend des analyses de la sensibilité des modèles de flux génétiques et de dynamique des populations, est nécessaire pour déterminer les types d'études à entreprendre afin de réduire l'incertitude actuelle.*

INTRODUCTION

Fish behavioural traits can shape the ecological interactions that occur with conspecifics. In addition, environment and genetics can influence behaviour such that variability is expected among fish of different backgrounds. Extreme differences in environment, and often genetics, are seen when farm fish are compared with those in the wild. The growth of Atlantic salmon farming worldwide, along with serious declines in wild populations in parts of the species' range, have brought concerns about such differences to the foreground. Knowledge of behavioural differences between farm and wild salmon will be vital to understand and mitigate the potential effect of escaped farm salmon on wild populations. For the purpose of this work, we define farm fish as those grown for the intended purpose of consumption. In comparison, fish raised for the purpose of stocking are termed "hatchery fish." Although both are raised in artificial environments, specific selection for certain traits is usually much stronger on farm fish than on hatchery fish. Here we review existing knowledge about the behavioural patterns of escaped farm salmon in nature and how such patterns may influence the potential for, and the outcome of, interactions with wild salmon. We review what is known of the behaviour of farm salmon escapees at three stages: (1) dispersion and migratory behaviour following escape; (2) breeding and interactions upon entering wild salmon rivers; and (3) subsequent offspring life history, behaviour and interactions with wild salmon.

BACKGROUND

Marine net pen farming of Atlantic salmon has grown rapidly since 1980, from a little less than 5,000 metric tons to over 1.1 million metric tons in 2004 (ICES 2005). Over two-thirds of the current production comes from two nations, Norway and Chile. Canada produced 110,464 metric tons of farm Atlantic salmon in 2004 or slightly less than 10% of the global production. Sixty-four percent of the Canadian production occurred in British Columbia, with the remaining 36% in the Atlantic Provinces. The outer Bay of Fundy, New Brunswick, is responsible for the vast majority of the Atlantic Canadian production (ca. 88%), with other regions, such as Bay d'Espoir and Fortune Bay, Newfoundland, producing at a much smaller scale (Statistics Canada 2004).

The rapid growth of marine net pen farming of Atlantic salmon has been accompanied by an increase in the numbers of escaped fish in the wild as a result of regular low-level "leakage", and episodic events such as storms. It is estimated that two million farm salmon escape each year into the North Atlantic (Schiermeier 2003). Although farm salmon may escape as juveniles from freshwater hatcheries (e.g., 51%–67% of the ca. 4,000 smolts emigrating from the Magaguadavic River, New Brunswick, in 1996 were juvenile escapees (Stokesbury and Lacroix 1997); see also Clifford et al. 1998), most reported escapes occur from marine net pens. In Norway, official statistics kept by the Norwegian Directorate of Fisheries indicate that between 368,000–730,000 farmed salmonids escaped annually during 2001–05. These should be considered minimum estimates, as evidence suggests some escapes go unreported (Fiske et al. 2006). The main causes of these escapes include inadequate operation procedures and staff training, and construction failure (Norwegian Directorate of Fisheries 2005). In British Columbia, official reports indicate that 58,952 Atlantic salmon escaped from freshwater facilities and 386,446 from marine facilities between 1992 and 2002 (Fisheries and Oceans Canada 2002). Net failure and losses from handling are responsible for the majority of the escape events (Whoriskey 2001). The frequency of escape events that have been documented, however, has been decreasing (Whoriskey et al. 2006), though numbers of escapees remain large. The most comprehensive data on escapees in nature come from Norway, where farm salmon have been found to constitute on average between 11% and 35% of the spawning populations, with some populations exceeding 80% farmed fish (Fiske et al. 2001). Moreover, it is estimated that during 1989–96 roughly 20% to 40% of the Atlantic salmon caught in the high seas fisheries north of the Faeroe Islands, a principal feeding ground, was of farmed origin (Hansen et al. 1999, Jacobsen et al. 2001, Hansen and Jacobsen 2003). In Atlantic Canada, the proportions of escapees within salmon populations close to net pen operations may range from lows of 2.3% (Dempson and Power 2004) to highs exceeding 80% (Carr et al. 1997a).

In the remainder of this report we examine the current state of knowledge regarding the behaviour and fate of escaped Atlantic salmon, and discuss the potential for interactions with wild populations.

DISPERSION AND MIGRATORY BEHAVIOUR OF ESCAPED FISH

Dispersion following escape

We are aware of only two studies that have examined the dispersion of farm salmonids immediately after escape in marine environments. Whoriskey et al. (2006) found that experimentally "escaped," sonically tagged, farm Atlantic salmon (75 released in winter [January] and 198 released in spring [April–May]) dispersed away from a cage site in Cobscook Bay, Maine, within a few hours after release. Moreover, the fish generally moved rapidly away from the coastal zone near the cage site and out to the Bay of Fundy. The majority of these fish followed the dominant tidal circulation of the region. In contrast, Bridger et al. (2001) found that triploid farm rainbow trout experimentally released into the fjord-like Bay d'Espoir area of Newfoundland tended to congregate in the vicinity of the culture cages. However, over time the fish did disperse, and this dispersal was more rapid in winter than summer. In both studies, the fish were reared in hatcheries near the cage sites (within 40 km) and thus likely to have had similar imprinting to nearby freshwater systems. The differences between the studies may reflect both species differences (including ploidy) and variation in the environmental conditions at the point of release. In the case of the Bay of Fundy region, the rapid dispersal of fish following an escape event would likely render gill nets or other recovery methods ineffective because they probably could not be organized and deployed quickly enough to recapture the fish while they were still concentrated around the cages.

Farm salmon escapees in the northeast Atlantic disperse widely in the marine environment and have been captured in large numbers in north of the Faeroe Islands (Hansen et al. 1999; Jacobsen et al. 2001; Hansen and Jacobsen 2003). They have also been captured as far away as West Greenland, though in far smaller numbers (Hansen et al. 1997). Indications from experimental "escapes" of salmon from farms in southwestern and mid Norway suggest the fish tend to move with the current as they disperse in the marine environment (Hansen 2006). By contrast, little is known of the scale of the marine dispersion of farm Atlantic salmon escaping in the northwest Atlantic.

In the Pacific, the scale of marine dispersion of farm Atlantic salmon also appears extensive, as fish escaping from farms in Washington State and southern British Columbia have been caught in fisheries ranging from Washington to Alaska (McKinnell and Thomson 1997; McKinnell et al. 1997; Brodeur and Busby 1998). Moreover, the escapees actively swam in the same direction as the residual surface currents (McKinnell and Thomson 1997).

Little is known about the dispersion of farm fish escaping at freshwater life stages from hatcheries. However, insight can be drawn from intentional releases of hatchery fish into rivers. Fish reared in high-density hatchery conditions, as occurs for fish destined for marine net pen farming, may fail to disperse into available habitat when released in large numbers (e.g. Symons 1969; Cresswell 1981). It would seem logical that hatchery fish would disperse less than wild fish given their rearing environment. However, it is unknown whether the freshwater dispersal behaviour of fish released or escaping from hatcheries differs from that of wild fish (Weber and Fausch 2003)

SURVIVAL AND FEEDING PERFORMANCE FOLLOWING ESCAPE

Our understanding of the fate of escaped farmed Atlantic salmon, whether they derive from hatcheries or marine net pens, remains incomplete (Whoriskey et al., 2006). Initially, the fish will be unfamiliar with the area they escape into and presumably have poorly developed survival skills (e.g., foraging, social and anti-predator behaviour). Moreover, they may escape at a time when local environmental conditions are poor (i.e. temperatures are harsh and feeding opportunities limited). For example, escapes from marine net pens often occur in the autumn and winter, when storms are most frequent and at a time wild salmon have migrated purposely to distant marine over-wintering areas. However, while the survival of escaped farm salmon might be expected to be low, significant numbers of escapees are regularly found entering rivers at spawning time (Lund et al. 1991; Webb et al. 1991, 1993; Carr et al. 1997a; Fiske et al. 2001, 2006; Whoriskey and Carr 2001) or captured in sea fisheries in the Atlantic Ocean (Hansen et al. 1999; Hansen and Jacobsen 2003).

Escaped farm salmon in the Atlantic generally appear to consume food resources similarly to wild salmon. Research fisheries north of the Faeroe Islands, a principal marine feeding ground for Atlantic salmon, found wild and farm salmon to have similar condition factors, suggesting that the escapees that had survived and migrated to this region had been able to adapt effectively to the wild environment (Jacobsen and Hansen 2001). They showed no differences in frequency, number or weight proportions of prey compared with wild salmon. Nor were there differences in diet. Moreover, a higher proportion of farm fish contained food items in their stomach than wild fish (57% compared to 51% during November–December and 85% compared to 76% during

February–March). Farmed salmon caught in Scottish coastal waters also appear to adapt to feeding on natural prey (Hislop and Webb 1992).

In contrast, gut analyses of marine-captured Atlantic salmon in the Pacific Ocean found only 21.3% of the escaped fish contained food items (McKinnell and Thomson 1997). This low feeding rate suggests that the escapees had a more difficult time adapting to the marine environment in the Pacific Ocean, which may have more to do with their non-native origin than their domestic origin.

Salmonid fish released or escaping into freshwater environments may show differences in feeding behaviour. However, results regarding such effects are more equivocal, potentially reflecting a time lag in adjustment to feeding on natural prey (Einum and Fleming 2001). Released fish may initially behave inappropriately after being introduced into a novel environment, but with time may acclimate to the local environment. For example, L'Abée-Lund and Langeland (1995) found that the diet of released brown trout initially differed from that of wild trout, but within the first summer the released fish adopted a similar diet (see also Johnsen and Ugedal 1986). As post-smolts, Atlantic salmon released or escaping from hatcheries can adapt well to local foraging conditions and in the Bay of Fundy and Gulf of Maine, and have been observed to contain more food items in their stomach, especially amphipods, krill and sand lances, than wild post-smolts (Lacroix and Knox 2005). Moreover, observations of wild and hatchery steelhead trout (*Oncorhynchus mykiss*) that were tagged acoustically as smolts show them to have fundamentally similar early marine survival (Welch et al. *in press*).

Survivorship of escaped farm Atlantic salmon appears to vary geographically and temporally. Hansen and Jacobsen (2003) reported that recoveries of farm and wild salmon in coastal and freshwater fisheries that had been tagged north of the Faeroe Islands 4–18 months earlier showed a broad geographical distribution. Recaptures of wild salmon ranged from northern Spain to Russia and as far away as Canada, and were far more widespread than recaptures of farm salmon, which were confined to Norway with the exception of one fish from Sweden. Also, wild fish (2.3%) were recovered at a significantly higher rate than farm salmon (1.2%). For both groups, recapture rates were greater for fish tagged in winter than in autumn. This likely reflects the longer time at sea for fish tagged in autumn and thus longer exposure to marine mortality factors. A similar pattern was observed in an experiment involving sequential releases ("escape") of individually tagged large farm salmon from two fish farms in Norway (Hansen, 2006). Recovery from the commercial and sport fisheries was extremely low for fish released in November from both farm sites (0.2%), but increased with time of release and reached 4.5–5.5% in March/April. It is unlikely, however, that length of time at liberty in the marine environment alone can explain these differences. Rather, environmental conditions at the time and location of escape may have played a significant role. Temperatures and/or feeding conditions in the late autumn can be particularly poor in coastal areas for salmon. It is a time when wild salmon have migrated to distant marine over-wintering grounds.

Evidence from the northwest Atlantic indicates that mortality can be very high immediately after escape and differ seasonally (winter to spring). In a series of experimental "escapes" of sonically tagged salmon from a farm in Cobscook Bay, USA, Whoriskey et al. (2006) recorded high mortalities within the bay and the surrounding coastal region (56–84% depending on season). Information based on discarded tags indicated that much of this mortality in the coastal zone was due to sea predation. Moreover, the seasonal pattern of mortality was consistent with the idea of seal predation being the primary cause of mortality.

The survival and performance of farm salmon escaping at freshwater life stages from hatcheries is likely to differ in many respects from wild fish. Einum and Fleming (2001) in a meta-analysis of literature data found that hatchery fish consistently experienced reduced survival in nature compared to wild fish (15 of 16 studies combined probabilities $\chi^2 = 109.15$, $df = 18$, $P < 0.001$). They concluded that the success of hatchery-produced fish after release or escape appears to be constrained by phenotypic divergence from their wild conspecifics (see below for further discussion). This is not surprising given the potential importance of local differences among wild salmonid populations in fitness-related traits (Taylor 1991; Garcia de Leaniz, *in press*) and the effects of hatchery environments on development and selection (Einum and Fleming 2001; Weber and Fausch 2003).

HOMING AND STRAYING TO RIVERS

It is well known that in salmon (*Salmo* and *Oncorhynchus*), cues encountered by the seaward migrating smolts influence their homing behaviour and river ascent (reviewed in Hansen and Quinn 1998). When sexually mature, wild and hatchery salmon enter rivers for spawning, and both may home to the area of origin (Jonsson et al. 1990, 2003). Parr escapes from freshwater facilities can result in high incidence of farm parr in some rivers on the Atlantic (Maguadavic River, New Brunswick: 51–62% [Stokesbury and Lacroix 1997]) and Pacific coasts (80 rivers [Volpe et al. 2000; Fisheries and Ocean Canada 2002]). Farm salmon that escape as juveniles from hatcheries have been observed to return to areas adjacent to the hatchery outflow (Clifford et al. 1998). Generally, the homing precision of fish that are released or escape from hatcheries appears less accurate than that of wild fish, even when the two leave the river together as smolts (Jonsson et al. 2003). As a rule of thumb, fish released at the wrong time and at the wrong site stray more – i.e. have poorer homing ability – than those released at more appropriate (natural) times and sites (reviewed by Quinn 1993).

Given the above, it is not surprising that the farm fish escaping from marine net pens show greater straying than those escaping from hatcheries. Hansen and Jonsson (1991) showed that reared fish kept in saltwater, tagged and released into a Norwegian fjord every month throughout a year, tended to return to the geographical area of release and enter nearby rivers to spawn, except when released in late winter when they tended to stray farther away from the release site. Older farm salmon escaping from net pens a year or so before spawning appear to exhibit even greater levels of straying. In a series of sequential releases ("escapes") of individually tagged large farm salmon from two fish farms in Norway, Hansen (2006) observed little evidence of a homing instinct to the site of escape. Freshwater recaptures of these fish were scattered in rivers from Sweden in the south, along the Norwegian coast to as far north as the Russian river Touluma. Hansen (2006) concluded that the large farm salmon in the experiment had limited imprinting to any particular river or marine site, and many of these fish appeared "homeless." Fish approaching maturity that escape, however, appear much more likely to enter rivers in the vicinity of escape (Lura and Sægrov 1991; Webb et al. 1991; Carr et al. 1997a; Dempson et al. 1999; Whoriskey et al. 2006). Moreover, results of a displacement experiment in New Brunswick documented a tendency for river fidelity in escaped farm salmon during their spawning migration (Whoriskey and Carr 2001). This may have been, in part, due to some fish having reared as juveniles in hatcheries located on the river. Comprehensive surveillance data from Norway (16 years [1989–2004] and 95 rivers surveyed periodically) indicates the existence a highly significant, positive correlation between the intensity of salmon farming and incidence of escapees in rivers in the nearby area (Fiske et al. 2006). Thus, wild populations close to large numbers of salmon farms are more susceptible to invasion by escapees than those farther away.

In the Pacific Ocean, farm Atlantic salmon having escaped from marine net pens similarly disperse broadly to rivers, some as far away as Alaska. However, the majority of freshwater recoveries of farm escapees occur in the vicinity of farming operations. In British Columbia, Atlantic salmon have been found in more than 80 rivers, although naturally reproduced feral juvenile populations have been found in only three locations (Volpe et al. 2000).

WITHIN RIVER MIGRATORY PATTERNS

Timing of river entry in Atlantic salmon appears to be delayed in fish that lack experience with their home river as juveniles (e.g., fish released from hatcheries or escaping from marine net pens: Jonsson et al. 1990, 1994; Skilbrei and Holm 1998), but this did not necessarily affect spawning time (Fleming et al. 1997). Not surprisingly, escaped farm fish in both the northeast (Lund et al. 1991; Thorstad et al. 1998) and northwest (Carr et al. 1997a) Atlantic Ocean frequently enter rivers after wild salmon, and sometimes after rod fisheries have closed.

The upstream migration of escaped farm salmon is probably influenced by the absence of directed migration to any particular spawning area. Experimental studies of radio-tagged wild and farmed salmon in the River Alta, northern Norway (Heggberget et al. 1993, 1996; Økland et al. 1995) and River Namsen, mid-Norway (Thorstad et al. 1998) showed similar patterns. Upon entering freshwater, farm and wild salmon had similar migratory speeds, though farm salmon distributed themselves higher up the river than wild salmon during spawning. In other rivers, however, farm salmon have been observed mainly in the lower parts, downstream of the majority of wild salmon (e.g., Power and McCleave 1980; Webb et al. 1991). In addition, farm salmon in the River Alta system tend to move to neighbouring streams and are distributed more randomly than wild fish (Heggberget et al. 1993). Farm salmon also appear to exhibit more up- and downstream movements during the spawning season than wild salmon (Thorstad et al. 1998; see also Jonsson et al. 1990, 1991), which may have reflected a lack of river imprinting or inferior competitive abilities (Fleming et al. 1996). Despite these differences, farm salmon frequently overlap with wild salmon during spawning (Webb et al. 1991, 1993; Økland et al. 1995; Heggberget et al. 1996; Thorstad et al. 1998; Fleming et al. 2000).

There is a striking difference in the migratory patterns of farm escapees in the northwest relative to the northeast Atlantic. In the Magaguadavic River, New Brunswick, the majority (85%) of escaped farm salmon entering are immature and will not spawn the year of freshwater entry (Lacroix et al. 1997). These non-maturing fish remain in the lower parts of the river and do not reach known spawning areas (Carr et al. 1997b). Why these non-maturing salmon entered fresh water remains unanswered.

CONCLUSIONS

The patterns of dispersion, survival and migratory behaviour described above set the stage for potential ecological and genetic interactions. Timing and the life stage at which salmon escape from net pens influence their likelihood to survive and "home" to local waters or disperse broadly. Evidence suggests that fish escaping as smolts or as adults nearing maturity are more likely to enter nearby rivers to spawn than are post-smolts escaping a year or more prior to maturity. Survival following escape is likely to be lower than that of comparable wild fish and particularly poor during late autumn and winter, when coastal conditions for salmon are inhospitable. Those fish that do survive appear fully capable of switching to natural prey, at least in the northeast Atlantic Ocean. Results from the northwest Atlantic and northeast Pacific Oceans, however, are equivocal. The evidence appears clear that wild salmon populations near intense salmon farm operations are more likely to be invaded by escapees than those populations further away. The timing of entry of farm escapees into rivers is often after the entry of wild fish, however, there is little indication that this influences the timing of spawning. Rather, the timing of spawning appears to be more population dependent, with reduced overlap in some populations (i.e. farm escapees tending to spawn a bit before or after local wild salmon) and full overlap in others. Similarly, spawning locations of escapees and local wild salmon may show full or reduced overlap. Despite some differences in spawning time and location, farm salmon frequently overlap with wild salmon during breeding that may lead to a series of ecological and genetic interactions.

Below, we focus on the behavioural patterns of farm salmon that can influence the likelihood and outcome of interactions with wild salmon in freshwater, the environment in which interactions are likely to be most intense. While behavioural patterns, particularly during reproduction, are a key determinant of the potential for genetic introgression and subsequent genetic effects, we focus on how such patterns influence the likelihood of ecological interactions. The subject of genetic effects is the focus of another review in this series and therefore we do not discuss it further here, but refer readers to other reviews of the subject (e.g., Hindar et al. 1991, 2006; Waples 1991; Youngson and Verspoor 1998; Ferguson et al., *in press*).

BREEDING PERFORMANCE, BEHAVIOUR AND INTERACTIONS

The behavioural and genetic effect of farm fish on wild populations is commonly first seen during breeding following migration into rivers from ocean net pens. Interbreeding with wild individuals, or breeding among farm males and females, can alter the genetic structure of wild populations, particularly if gene flow occurs. However, prior to gene exchange, salmon undergo a series of behavioural interactions and life-history processes that will ultimately determine their reproductive success. In the following section, we examine the spawning characteristics of farm salmon, and how they compare with wild fish.

FEMALE SPAWNING CHARACTERISTICS

Fecundity in salmonid fish generally increases with body size, however, this allometric relationship appears to differ between artificially cultured and wild salmonids (e.g., Fleming and Gross 1990; Jonsson et al. 1996; Heath et al. 2003). For example, female farm salmon frequently have greater fecundities and smaller egg sizes for a given body size than wild females (e.g., Fleming et al. 1996; Heath et al. 2003; Fleming et al. 2003).

The eggs of female salmon are deposited in a series of nests on the spawning grounds. The nests are a depression created in the streambed through a series of tail beats. A female usually digs a series of several nests, called a "redd," and the number of eggs deposited in each subsequent nest generally decreases (Fleming 1996). Female salmonids may fight for access to favorable spawning sites, though escalated aggression is more common in the semelparous (Pacific salmon) than iteroparous species, such as Atlantic salmon (Fleming 1998). There is no evidence that farm and wild Atlantic salmon females differ in aggression during spawning in semi-natural conditions (Fleming et al. 1996). Some studies, however, indicate that farm females tend to construct fewer nests (Lura et al. 1993; Fleming et al. 1996, 2000) and deposit fewer eggs per nest (Lura et al. 1993) than do wild females, while others report that characteristics such as the dimensions of the redd (Lura et al. 1993), number of nests (Økland et al. 1995), and eggs per nest (Fleming et al. 1996) do not differ. Farm females have been observed to have greater egg retention (Fleming et al. 1996) and consequently a lower potential egg deposition (McGinnity et al. 2003) than wild females. In addition, farm females may not perform as much digging behaviour as wild females (Fleming et al. 1996).

Individuals of farm origin may spawn earlier and for shorter periods of time than wild females, as determined by release experiments as well as experiments in semi-natural conditions (Fleming et al. 1996, 2000). However, one study examining the spawning behaviour of escaped fish observed that farm females spawn later in the season than do wild females (Webb et al. 1991, 1993). This is of particular concern because farm and wild females can choose similar spawning locations when they are found together (Fleming et al. 2000), and later spawning by farm females may result in superimposition of nests constructed by wild females and affect development and survival of eggs deposited earlier in the season. Farm females tend to have a more limited distribution in rivers, where they are found in larger numbers either downstream (Webb et al. 1991,

1993) or upstream (Økland et al. 1995, Thorstad et al. 1998) from concentrations of wild salmon (however, Fleming et al. (2000) saw no difference in farm and wild female distribution in a small river system). Farmed fish also tend to have greater movement within rivers (Økland et al. 1995, Thorstad et al. 1998), and stray to smaller rivers (Heggberget et al. 1993). Overlap in spawning areas used by farm and wild females may result in decreased reproductive success of wild females if farm fish are present because farm females can adequately compete for spawning sites. While available evidence indicates that overlap is not complete, later spawning by farm females can result in superimposition of redds constructed by wild females and have a major effect on wild fish production. Furthermore, from a purely demographic perspective, spawning by farm females results in fewer offspring produced, due to fecundity differences between wild and aquaculture fish (e.g. Jonsson et al. 1996, Heath et al. 2003). Although farm females tend to be less successful than wild females, gene flow from farm fish into wild populations via females is likely due to their relatively high competitive ability.

MALE SPAWNING CHARACTERISTICS

The aquaculture environment can lead to altered expression of secondary sexual characteristics (Fleming et al. 1994; Hard et al. 2000). This is important in light of the fact that studies on salmonids have highlighted the potential importance of secondary sexual characters for male-male competition (Fleming and Gross 1994) and female choice during mating (Quinn and Foote 1994; Petersson et al. 1999). Differences in spawning behaviour between farm and wild fish were more pronounced in males than in females. Large farm males tended to be less aggressive and courted females less often when in direct competition with wild males (Fleming et al. 1996, 2000). In this species, the aggressive, dominant males in a group are expected to court females the most frequently, participate in more solo spawnings, and realize the highest reproductive success (Jones 1959). However, when competing in pure groups, farm males had larger courting and spawning group sizes, but less reliable behavioural correlates of spawning success than wild males (Weir et al. 2004). Webb et al. (1991) found that farm males tended to increase courtship in the later part of the spawning season, indicating that there may be a genetic component to the timing of breeding, or that they are capitalizing on the spawning fatigue of wild males that may occur in the later part of the spawning season (Fleming 1996).

The effect of the aquaculture environment on male breeding behaviour is likely due to both environmental and genetic factors. Farm males do not differ behaviourally from their wild progenitors when both are raised in captive conditions, as the environmental effect of captive rearing swamped potential genetic differences (I.A. Fleming and S. Einum, unpublished; see also Bessey et al. 2004). More studies aimed directly at disentangling the environmental effects from genetic effects on spawning behaviour are needed.

As expected, based on differences in male behaviour, the spawning success of farm males was generally lower than that of wild males (Fleming et al. 1996, 2000, Weir et al. 2004). The effect of large farm males on the spawning grounds may be manifested in reduced fitness for females who mate with them. Despite being competitively inferior to wild males, the presence of farm males in large numbers on spawning grounds may interfere with spawning even if farm males do not mate. However, compared to females large farm males may not represent the primary means of gene flow between farm and wild fish, though they can have both direct and indirect effects on wild fish fitness.

Salmonid males can mature at different life stages. In Atlantic salmon, males may mature as large, usually migratory individuals, or as small parr that have not yet migrated to sea. The latter represent a secondary means by which farm fish genes may enter wild populations. Only two studies have examined the reproductive success of mature male parr, and both indicate that parr of farm origin may have had higher fertilization success than wild individuals (Garant et al. 2003; Weir et al. 2005 (F_1 hybrids only)), and were present in greater (Garant et al. 2003) or similar numbers (Weir et al. 2005) to wild parr during specific spawning events. However, there was no evidence that aggression was higher in mature farm parr (Weir et al. 2005). As farm parr success is similar to or even greater than that of wild parr, they represent a route of introgression of farm genes into wild populations that can occur over a very short period of time. This is of particular concern because of the shifting demographics in some populations whereby there are fewer large individuals returning to the rivers to spawn (Parrish et al. 1998).

AGE AT MATURITY

Age at maturity of farm fish varies among studies, possibly reflecting both a specific genetic component in age at maturity within river systems, and the selection in the farm environment for later age and larger size at sexual maturity. It is important to note that among wild populations, there is considerable variation age at maturity (e.g. Hutchings and Jones 1998, Klemetsen et al. 2003), reflecting the importance of considering which farm and wild populations are being compared. Sea age, body size and condition at maturity did not differ among farm and hybrid fish in the study conducted by Fleming et al. (2000). However, relative to wild salmon, McGinnity et al. (2003) found farm and hybrid salmon generated higher numbers of 2 sea winter (SW) returns, but lower numbers of the naturally occurring 1 SW returns farm and hybrid salmon. In addition, Fleming et al. (2000) reported an earlier mean age at maturity for farm-wild hybrid fish. Similarly, Lura and Sægrov (1993) reported that timing of maturation is earlier in farm females than wild females, and farm females were smaller at the time of spawning. Farm parr exhibited lower incidence of maturity than did wild parr (Fleming and Einum 1997, McGinnity et al. 1997), reflecting selection against this trait in breeding programmes (Gjerde 1984). Earlier age at maturity could lead to faster generation times for farm fish, thereby increasing the rate of gene flow from farm to wild populations. Furthermore, changes in age at maturity of farm fish, such as those seen by McGinnity et al. (2003), can significantly alter the demographics of a given population.

SURVIVORSHIP DURING AND FOLLOWING BREEDING

Farm fish generally experience higher mortality than wild fish during breeding. Experimental studies indicate that farm male mortality is quite high during breeding and can range from 50% to 100%, whereas farm female mortality is lower, ranging from 0% to 42% (Fleming et al. 1996, Weir et al. 2004). In addition, behavioural differences may be more pronounced in individuals raised in sea cages (Fleming et al. 1996) than in those reared in freshwater (Weir et al. 2004). However, Thorstad et al. (1998) report higher post-spawning survival in farm fish relative to wild in a release study. Mortality during spawning of mature male parr does not differ among fish of wild or farm origin (Weir et al. 2005).

MATERNAL EFFECTS ON OFFSPRING

Egg survival in fish of farm origin was similar (McGinnity et al. 2003) or lower (F_2 hybrids: McGinnity et al. 2003) than that of wild fish in natural conditions. Furthermore, Lura and Sægrov (1993), found that farm offspring hatch rate in the wild was lower than that of wild fish. Offspring survival may be further compromised by maternal effects on size at hatch due to smaller egg size (Einum and Fleming 2000a, Fleming et al. 2000). Individuals that were smaller at hatch generally tended to have lower survival subsequently (Einum and Fleming 2000b). Juvenile survival in rivers tended to be lower among fish of farm origin than among fish of wild origin, which is likely due to both non-genetic maternal effects and heritable differences (McGinnity et al. 1997, 2003, Fleming et al. 2000). Furthermore, farm females tend to spawn later than wild females, which may result in a competitive disadvantage for their offspring. Spawning locations of farm females are also more limited than those of wild females, such that in the wild, escaped farm offspring are more concentrated in certain areas of the river.

CONCLUSIONS

In summary, farm females are generally successful when compared with wild fish during spawning in natural or semi-natural conditions. Farm females may affect wild offspring output, as they can spawn in the same location as wild females, and may adversely affect the survival of wild offspring. In addition, timing of reproduction often differs, which can affect wild population structure. Within populations of Pacific salmon, there are important differences in spawning times (e.g. Boatright et al. 2004; McLean et al. 2005), such that interbreeding among different groups may upset particular spawning times. While some aspects of female behaviour differ, the more pronounced effect of the farm environment is observed among males. Large males are generally unsuccessful and have poor survival during and following spawning in rivers and in semi-natural experiments. Wild males in many populations do not survive more than one spawning season (Fleming 1998), however farm males generally fail to behave appropriately during the spawning period. While they may be out-competed by wild males in situations where there are equal numbers of farmed and wild males (Fleming et al. 1996), if major escape events result in farm males vastly outnumbering wild males there could be extreme consequences in terms of wild population numbers. Conversely, mature male parr of farm origin are more successful relative to wild parr and represent a secondary means of genetic introgression that may occur over a shorter period due to their shorter generation time (Garant et al. 2003). In addition, younger ages and/or larger sizes at maturity among adult fish can also speed up the rate at which spawning wild populations are exposed to genes from the farm environment. The likelihood of fertilization by parr of farm origin is complicated by the fact that the incidence of male parr maturity has been found to be lower among farm parr than it is among wild parr (Einum and Fleming 1997, McGinnity et al. 1997). Regardless, farm fish can and do interact with wild fish during the spawning period.

OFFSPRING SURVIVAL AND PERFORMANCE

Following successful breeding, or escape from freshwater facilities, behavioural and life-history characteristics of farm offspring (and farm-x-wild hybrids) will influence their survival and performance in the natural environment. Any differences between farm and wild individuals at early life stages may be a result of genetic and/or environmental effects. In the case of the former, genetic effects are most likely to be a significant influence if juveniles are present in river systems as a result of spawning activities of escaped adults, particularly if they are not native stock. Maternal effects play a large role in the early success of juveniles (e.g. Einum and Fleming 2000b). Environmental effects may be manifested if juveniles escape from freshwater facilities and lack early experience in the river system. Below, we describe behaviour and life-history characteristics of juvenile salmon of farm and wild origin.

DIET/FORAGING/HABITAT SELECTION

Lura and Sægrov (1993) found that newly emerged farm fish begin to feed at lower temperatures than do wild fish. This suggests that although farm origin fish may be smaller at hatch, they may begin feeding earlier, and thus may have an advantage over wild fish in rivers at a very early life stage. Furthermore, juveniles of farm, wild and hybrid origin do not have drastically different diets in the wild (Einum and Fleming 1997; Fleming et al. 2000), which suggests that they could compete for the same resources as wild fish. On the west coast of Canada, the stomach contents of the offspring of escaped farm Atlantic salmon were similar to those of rainbow trout juveniles, but the farm juveniles grew 1.5 and 2.3 times faster at age 0 and 1, respectively, than the trout (Volpe et al. 2000).

The results regarding farm fish (Einum and Fleming 1997; Fleming et al. 2000; Volpe et al. 2000), however, contrast with studies of hatchery-reared salmonids. In the former case, the fish are commonly born into the wild, being the offspring of successful farm spawners; whereas in the latter case the fish are released from captivity having experienced only the hatchery environment. The hatchery-reared fish are in many ways equivalent to farm fish escaping as juveniles from freshwater rearing facilities. In a review of the literature, Weber and Fausch (2003) concluded that some such fish are unable to learn to forage for prey found in stream environments (based on studies by Elliott 1975; Maynard et al. 1996; Olla et al. 1998) or eat less food (e.g. Sosiak et al. 1979; Ersbak and Haase 1983; Smirnov et al. 1994) and fewer prey types (Sosiak et al. 1979) than wild fish. Alternatively, they may consume similar prey items as wild fish but switch to new types of prey more slowly, as the type and amount of invertebrate taxa available change seasonally. Salmonids reared in hatcheries also tend to consume fewer benthic invertebrates than wild salmonids (Sosiak et al. 1979; Maynard et al. 1996), because they often occupy space closer to the water surface (Weber and Fausch 2003). As such, they also consume terrestrial insects (Johnsson et al. 1996). Similarly, Mork et al. (1999) found that hatchery salmon spend more time feeding in the water column and more time inactive than wild fish.

At the smolt stage, food consumption does not differ significantly between farm and wild fish raised in the hatchery environment, however, food conversion efficiency was higher within farm fish (Handeland et al. 2003), a trait likely selected for during artificial breeding. Stomach content analysis of smolts captured in the wild during the marine phase also suggested that there were no significant differences between farm and wild fish diet (Jacobsen and Hansen 2001). However, LaCroix and Knox (2005) found that fish of hatchery origin had a tendency to consume more, and different, prey.

While distribution of juvenile farm and wild salmon has not been extensively studied, there are only subtle differences in their distribution in rivers (Einum and Fleming 1997). No differences in current or depth occupied were found, however Einum and Fleming (1997) observed that farm fish tended to be found in slower moving parts of the stream environment. Studies of hatchery fish vary with respect to habitat use. Mesa (1991) found that hatchery cutthroat trout occupied faster flowing water than did wild trout. However, Greenberg (1992) and Lachance and Magnan (1990) found no differences in habitat use between wild and hatchery brown trout and brook trout, respectively. As stated above, Mork et al. (1999 [also reviewed in Weber and Fausch (2003)]) found that hatchery origin fish tended to forage higher in the water column than did wild fish.

These studies suggest that farm and hybrid fish have the potential to compete with wild fish for similar food resources, although experiments using hatchery fish suggest that the overlap may not be complete. Furthermore, farm or hatchery juveniles may differ from wild individuals in distribution within rivers and within feeding territories; however these differences are usually not extreme, which indicates that they may on occasion not be competing within the same microhabitat. Regardless, the presence of farm and hybrid juveniles in the river environment limits food and habitat resources for wild fish.

GROWTH RATE

There is an overall tendency for farm and hybrid juveniles of a given age to be larger than their wild counterparts (Einum and Fleming 1997; Fleming and Einum 1997; McGinnity et al. 1997, 2003; Fleming et al. 2000, 2002), as would be expected after selection for fast growth in aquaculture. Some studies suggest that differences in growth are associated with endocrinological change (Fleming et al. 2002). For example, faster growth of age-1 farm juveniles relative to wild individuals is associated with increased growth hormone in farm fish. However, this difference was age and stage dependent, and there were no significant differences between farm and wild fish with respect to insulin growth factor 1, which indirectly affects growth rate (Fleming et al. 2002). Interestingly, Fleming et al. (2002) also found that discrepancies in growth rate between farm and wild juveniles (age 2+) are most evident in salt water. Seawater tolerance of farm and wild origin smolt has been shown to be lower among the former when raised under similar conditions, however farm fish growth was higher than that of wild fish in seawater following acclimation (Handeland et al. 2003). Age at smoltification was younger (Fleming et al. 2000), or similar (McGinnity et al. 2003) to wild fish in the natural environment. However, weight and length at smoltification tended to be higher among farm and hybrid fish in both hatchery (Fleming and Einum 1997; Thodesen et al. 1999; Handeland et al. 2003) and river environments (Fleming et al. 2000). Faster growth of farm juveniles may lead to dominance over wild individuals due to larger body size (e.g. Wankowski and Thorpe 1979), although the causal nature of this relationship is not yet clear (Huntingford et al. 1990). However, faster juvenile growth of farm individuals leads to higher food consumption and earlier age at smoltification. This may result in limiting resources for wild fish and upset wild population demographics (McGinnity et al. 1997, 2003; Fleming et al. 2000).

AGGRESSION/DOMINANCE

Dominance, or aggression, is usually associated with faster growth (Mesa 1991). Salmonid juveniles in the wild hold feeding territories that they defend from intruders. Farm and hybrid juveniles also tend to be more aggressive than wild fish, however this is dependent upon the origin of the wild and farm fish. For example, Einum and Fleming (1997) found that juvenile aggression was higher among farm fish than wild fish from the Imsa River, Norway, but not higher than wild fish from the Lone River, Norway, when the fish competed for food in laboratory pair-wise contests. This suggests that the outcome of interactions between farm and wild fish may be context-dependent. Furthermore, Fleming and Einum (1997) found that farm fish were more aggressive in pure groups than when mixed with wild fish. Interestingly, farm fish aggression was lower than wild fish aggression in a stream environment, but similar to wild fish in a tank environment (Fleming and Einum 1997). Similarly, Metcalfe et al. (2003) found that farm fish were dominant over wild fish in pair-wise contests in a tank environment if both were raised in a hatchery environment. However, fish of wild origin could dominate farm fish when they had a prior residency time of two days. Interestingly, wild-origin fish that spent some time in a natural environment could also dominate both wild and farm fish raised in a farm environment (Metcalfe et al. 2003). Furthermore, experiments investigating the role of prior residency indicate that growth and territory holding potential is higher in fish introduced earlier (e.g. Rhodes and Quinn 1998; Cutts et al. 1999; Deverill et al. 1999), although prior residency does not always lead to increased dominance (O'Connor et al. 2000). However, intruders that are larger than residents may be able to effectively displace residents because of a body size advantage (Rhodes and Quinn 1998).

Data on interactions between Atlantic salmon juveniles and steelhead trout suggested that farm Atlantic salmon were more aggressive than steelhead, and less aggressive toward conspecifics than steelhead trout when in mixed groups (Volpe et al. 2001). In addition, experiments using different densities of steelhead trout and Atlantic salmon suggest that steelhead trout increase aggression with density, while Atlantic salmon do not, presumably because Atlantic salmon aggression levels were higher even at low densities (Volpe et al. 2001).

The outcome of aggressive interactions between wild and farm fish depends upon the environment and genetic background of the competitors. Wild fish can generally out-compete farm fish in simulated natural environments, particularly if they have prior residency advantage because they hatch earlier than farm juveniles or because farm fish enter the river environment following escape from freshwater aquaculture facilities. However, in the latter case larger body size of farm juveniles may enable them to displace wild fish from their territories (Rhodes and Quinn 1998).

PREDATOR AVOIDANCE

Some studies (Einum and Fleming 1997; Fleming and Einum 1997) indicate that farm fish are less effective at avoiding predators than are wild fish, and that their physiological response to predators, in terms of heart rate, is reduced (Johnsson et al. 2001). Specifically, time to hiding from predators is similar between farm and wild salmon, but farm salmon emerge from hiding more quickly than do wild fish (Fleming and Einum 1997). However, Johnsson et al. (2001) measured predator avoidance in terms of flight reaction, time to reaction, and distance to the predator in two age classes of juvenile Atlantic salmon (ages 1+ and 2+) that were exposed to predator attacks on two occasions in a hatchery environment. While they found very few behavioural differences between hatchery-raised farm and wild fish, younger farm fish had shorter flight duration than wild fish on the first predator attack, and distance to the predator was longer for younger farm fish. No differences were observed in the older age class. In a recent study, Biro et al. (2004) released hatchery-raised farm and wild rainbow trout into lakes with natural loon predators. Farm trout avoided predators less effectively than did wild trout, and had lower survival when in lakes with high predation risk. However, they had higher survival than wild fish in lakes with low predation pressure, and higher growth rate in lakes with high predation pressure. Overall, there are some differences in predator avoidance behaviour between wild and farm fish, suggesting that the latter may have reduced survival in the wild because they cannot effectively evade predators. In addition, hormonal differences may require that farm fish consume more food, and are more likely to risk predation to maintain growth (see discussion above for Growth Rate).

CONCLUSIONS

At juvenile stages, feral farm fish and feral farm-x-wild hybrids can be expected to interact and compete directly with wild fish. They are generally more aggressive and consume similar resources. In addition, they grow faster than wild fish and as such may be able to compete even more effectively for favorable feeding territories. While some studies show that farm fish may be less effective at avoiding predators than wild fish, this is not always the case. The effects of farm fish on wild populations and resources are likely very pronounced at younger life stages, when farm individuals have more experience in natural conditions and are able to adjust behaviourally and compete effectively for food and space. The competitive ability of farm fish during the juvenile stages can lead to depression of wild populations. Fleming et al. (2000) report that wild fish in the River Imsa had a 30% reduction in smolt production when farm fish were present in the rivers, despite that farm fish had only 19% success during spawning. This indicates that farm juveniles can have a substantial effect on survival of wild fish, even in small numbers. Similarly, McGinnity et al. (1997, 2003) found that while farm and hybrid juveniles frequently had lower survival than farm fish, they appeared to be displacing wild juveniles from the river. The presence of farm juveniles is likely to affect resource availability for wild fish, particularly if space and food are limiting. As such, behavioural interactions at juvenile stages are likely to have a significant effect on wild populations that have been invaded, particularly if the farm juveniles are hatched in the natural environment.

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OVERVIEW OF THE ENVIRONMENTAL IMPACTS OF CANADIAN FRESHWATER AQUACULTURE

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EXECUTIVE SUMMARY

Worldwide, aquaculture operations have been linked to a number of environmental effects that include nutrient enrichment, habitat alteration, and damage to wild fish populations (Gross 1998). A sound scientific understanding of potential effects on the freshwater environment is required if the industry is to grow in an environmentally sustainable fashion. This document provides an overview of the current state of scientific knowledge of the environmental effects of Canadian freshwater aquaculture activities, and identifies areas for future research. The use and potential environmental influence of chemotherapeutants is outside the scope of this review. World literature that is relevant to aquaculture practices occurring in Canada has been included because the scientific literature dealing expressly with Canadian freshwater aquaculture is extremely limited. Substantial changes in husbandry techniques have occurred in the aquaculture industry and these changes have rendered older publications less relevant to the current experience. Wherever possible, we have limited review to peer-reviewed scientific information published within the last decade.

The effects of aquaculture are complex and related to the production and release of organic waste materials as well as the interactions between cultured species and wild species. The bulk of aquaculture waste constitutes fish metabolic wastes and uneaten feed. Factors affecting waste production include fish size, water temperature, and husbandry practices (i.e., feed composition, ration, and feeding methods). The primary environmental concerns associated with waste generation are the potential for nutrient-induced stimulation of local algal blooms and the creation of hypoxic waters and sediments underlying net pens. The primary mechanism through which escaped fish affect native freshwater fish species is competition for limited resources and predation.

The primary constituent of solid wastes is faecal material with waste feed a secondary and much smaller component (Ackefors and Enell 1990). Faecal production, which is difficult to estimate accurately, ranges from 15% to 30% of applied feed (Costello et al. 1996; Cho and Bureau 2001; Bureau et al. 2003). Waste feed estimates, which are rarely reported, constitute between 3–40% of feed (Weston et al. 1996), and anecdotal reports and modeled predictions suggest that waste feed at Canadian farms is currently approximately 5%. There is a gap in data regarding feed waste. Solid wastes settle to the lake bottom where they are consumed by biota (Johansson et al. 1998) or decompose. The greatest accumulation occurs directly under cages (Enell and Lof 1983a), suggesting that direct effects on sediments may be geographically restricted. Sediments beneath fish cages generally show enrichment in phosphorus, nitrogen, organic carbon, and zinc

(Cornel and Whoriskey 1993; Kelly 1993; MacIsaac and Stockner 1995; and Troell and Berg 1997). Although there is extensive literature on the benthic effects of marine aquaculture, few recent publications document the benthic effects of freshwater aquaculture. Few peer-reviewed Canadian studies have been published within the last decade. Effects of fish farm wastes may be similar to those associated with other forms of organic enrichment, including decreased taxa richness and diversity, and increased abundance and dominance of organisms resistant to sedimentation and low oxygen availability (Hynes 1963; Johnson et al. 1993). Generally, effects on the sediments and benthic community are restricted to areas directly under the pens and a small distance away. There are no published studies of the recovery of sediments and sediment-associated communities at former Canadian farm sites. In Scottish freshwater lakes, significant alterations of benthic communities below cage sites were still apparent more than 3 years after cessation of farming (Doughty and McPhail 1995). Recovery of lotic systems from fish farm emissions is generally more rapid than in lentic systems, due to the increased dispersion of wastes by water flow and the relatively swift re-colonization by invertebrate drift (Doughty and McPhail 1995).

Dissolved carbon, nitrogen and phosphorus are released into the water column by solubilization from feed and faeces, and through the gill and urinary excretions of fish (Bureau and Cho 1999). Approximately 3 to 10 kg of phosphorus and 39 to 55 kg of nitrogen are released to the environment for every metric ton of fish that is produced (Ackefors and Enell 1994; Cho et al. 1994; Bureau et al. 2003). The majority of phosphorus in farm wastes is lost to sediments as solids (Enell and Ackefors 1991; Phillips, et al. 1993). Nitrogenous wastes, particularly ammonia and urea, form the largest component of the dissolved waste fraction. In general, detectable increases in water column ammonium or ammonia concentrations are reported in the vicinity of cages (NCC 1990) and in receiving waters downstream of land-based facilities (Selong and Helfrich 1998). There are no published reports of concentrations exceeding local water quality guidelines or causing toxicity, and concentrations downstream of land-based facilities are reported to return to background levels 400 m to 12 km from cages (Selong and Helfrich 1998). Cage farms that are located in shallow basins or basins with poor flushing have often reported detectable increases in total phosphorus, while farms located over deep water and with adequate flushing have generally reported no detectable change. Several studies have reported elevated phosphate in waters receiving effluent from land-based farms (Munro et al. 1985; Trojanowski 1990). The decomposition of solid waste accumulations results in the release of labile P to the water column (Kelly 1992; Kelly 1993). During periods of stratification, phosphorus released from sediments into hypolimnetic water will not be available for primary production. There has been little research into the cycling of P between farm waste accumulations and the water column, and the proportion of this P that is eventually available for primary production is unknown. This knowledge would be of significant value to the sustainable management of the industry.

Decomposition of wastes may result in hypoxia in sediments and the water column (Axler et al. 1998) but these outcomes have been rarely reported. Respiration by cultured fish may produce localized reductions in dissolved oxygen concentrations. Reports of reductions in dissolved oxygen concentrations in the vicinity of net pens are variable, but for the most part reductions are minor and of short duration at sites with adequate water exchange (Weston et al. 1996; Demir et al. 2001; Veenstra et al. 2003). A single study in the primary literature has provided *limited data about dissolved oxygen profiles at Canadian cage farms in the last decade (Hamblin and Gale 2002), suggesting that the collection and compilation of these data from Canada is required. The biological and chemical oxygen demand of wastes discharged from land-based aquaculture facilities can reduce dissolved oxygen concentrations in lotic waters for short distances downstream, however there are no recent Canadian data.*

Stimulation of pelagic bacterial populations may result from nitrogen, phosphorus, and organic carbon in dissolved metabolic wastes and leaching from faeces and feed. A single study investigating effects on pelagic microbial communities reported no increase in the abundance of bacteria near net pens in British Columbia, but significantly higher production (MacIsaac and Stockner 1995). Microbal stimulation has been observed in lotic waters receiving fish farm effluents. For example, river water and sediments downstream of fish farm effluent outfalls in New England showed a significant increase in bacteria abundance and heterotrophic activity when compared to control sites (Carr and Goulder 1990a).

Studies in Canadian lakes have thus far found no differences in chlorophyll a concentrations between control and farm sites (Cornel and Whoriskey 1993) and only localized effects on periphytic algae (MacIsaac and Stockner 1995). In addition to stimulating production in bacterial populations, the release of nutrients from aquaculture facilities can enhance primary production (Kelly 1993). In Finland, fish farm emissions into a lake resulted in significant increases in chlorophyll a and primary productivity and changes in species composition of phytoplankton (Eloranta and Palomaki 1986). Primary productivity in rivers can be stimulated by discharges from land-based facilities (Carr and Goulder 1990b). For example, Munro et al. (1985) reported a significant increase in epilithic algal biomass, chlorophyll a, and changes in algal species composition downstream of hatcheries in several British Columbia streams.

There are no published studies on the effects of freshwater cage-culture operations on native fish communities in Canada. The potential influences of cage operations on native fish communities include trophic alterations and interactions between native and farmed fish. In Canadian freshwaters, cage-culture generally occurs in oligotrophic systems. Nutrient enrichment of oligotrophic systems can lead to greater in-lake growth of native and stocked fish species (Stockner and MacIsaac 1996). Further trophic changes in native fish species can occur through the consumption of waste feed and faeces. Consumption of wastes by biota may reduce the localized effects of waste build-up under pens but there have been no attempts to quantify this mechanism in Canadian ecosystems.

Cage farming inevitably results in a small number of escaped fish, even in the absence of any catastrophic containment failure. The causes of escape include storm damage, collisions, predator attacks, vandalism and accidental losses associated with fish handling. There are no published estimates of the numbers of farmed fish that escape freshwater net pens in Canada. Studies in other countries have estimated that escaped fish within given freshwaters represent approximately 3% to 5% of total cage production (Phillips et al. 1985b). Predation and the competition for limited resources are the principal ways that escaped fish can alter the native fish community. The introduction of a new species, or greater numbers of a species already present, into an ecosystem results in some redistribution of resources among the fish community. The characteristics that favor certain species for aquaculture are the same ones that may allow *these species to flourish when introduced into foreign water bodies (i.e., generalists with broad environmental tolerances). However, there are no published studies that provide information on the survival of escaped fish in North American freshwater ecosystems.*

Species interactions, especially those from the establishment of self-sustaining introduced species or the alteration of indigenous gene pools, are potentially damaging consequences of aquaculture. The escape of farmed salmonids is not necessarily equivalent to the intentional introduction of the same species for management purposes. Agencies responsible for stocking programs may have different selection criteria and thus prefer different broodstock than that selected for farmed fish. The traits selected for aquaculture programs differ significantly from those required for survival in the wild (Bridger and Garber 2002) and divergence in behavior between native and domesticated fish increases with time in captivity. Interactions between escaped farmed fish and wild fish may be very different than interactions between native fish and stocked hatchery fish that have established self-sustaining populations, depending upon how much selection has occurred in the broodstock. The extent of any permanent effect of escaped farmed species depends on successful reproduction in the wild with other farmed, hatchery, or native fish of the same species, or through hybridization with closely related species. Interbreeding of farmed and native fish or farmed and naturalized stocked fish can produce long-term genetic changes in these populations that can be detrimental (McGinnity et al. 1997; Fleming et al. 2000).

KNOWLEDGE GAPS AND RESEARCH PRIORITIES

The environmental effects of marine aquaculture are fairly well documented, but little research has been done on the environmental effects of freshwater aquaculture on Canadian ecosystems, and such studies have been extremely limited elsewhere. Research is needed in the areas listed below.

- *There is need for knowledge about the factors that determine the amount of accumulation or the fate of bottom deposits in freshwater ecosystems. Information regarding current waste feed levels and feed conversion ratios at commercial freshwater finfish facilities in Canada is required to support this research.*

- *Research is needed to determine what effects freshwater aquaculture activities have on benthic habitats and communities. Research is also required to elucidate the relationship between amount of waste deposition and the severity of effects on benthic communities.*

- *There is a need to research the recovery of sediments and sediment-associated biota after fish farming has ceased.*

- *Research is needed to develop an understanding of how phosphorus, nitrogen and carbon from aquaculture facilities cycle in the freshwater environment to determine the ecological consequences of these subsidies.*

- *There is a need for knowledge about the effects of aquaculture wastes on the species composition, biomass, and productivity of primary producers, microbial communities, zooplankton, and native fish populations.*

- *Research is needed to determine the role of native (and escaped) fish in the removal and dispersion of phosphorus through consumption of waste feed and faeces. This information will improve the ability to estimate the proportion of waste phosphorus that becomes available to affect primary production.*

- *There is need for knowledge about the effects of all life-history stages of escaped fish in Canadian aquatic ecosystems. Accurate documentation on the number of escaped fish entering freshwater systems and a determination of the degree and outcome of wild, stocked and farmed fish ecological and genetic interactions is needed to support this research.*

UN APERÇU GÉNÉRAL DES IMPACTS ÉCOLOGIQUES D'AQUACULTURE D'EAU DOUCE EN CANADA

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SOMMAIRE

À l'échelon mondial, l'aquaculture a été liée à diverses incidences environnementales, notamment l'enrichissement en matières nutritives, la perturbation d'habitats et des dommages aux populations de poissons sauvages (Gross, 1998). Le développement écologiquement durable de l'industrie en eau douce exige des connaissances scientifiques solides des incidences potentielles sur ce milieu. Nous faisons dans le présent document un bilan de l'état actuel des connaissances scientifiques sur les incidences environnementales de l'aquaculture d'eau douce au Canada et nous identifions également des sujets de recherche futurs. L'utilisation et les incidences environnementales potentielles d'agents chimiothérapeutiques débordent cependant le cadre de ce bilan et n'y sont donc pas inclus. Nous y incluons les études étrangères pertinentes aux pratiques aquacoles canadiennes car la littérature scientifique traitant expressément de l'aquaculture d'eau douce au Canada est extrêmement rare. D'importants changements ont été apportés aux méthodes d'élevage, ce qui fait que les vieilles publications ne s'appliquent pas à ce qui se passe aujourd'hui. Dans toute la mesure du possible, nous avons limité notre examen aux documents scientifiques évalués par les pairs publiés au cours de la dernière décennie.

Les incidences de l'aquaculture sont complexes. Elles résultent de la production et du rejet de débris organiques, ainsi que des interactions entre les espèces d'élevage et les espèces sauvages. La masse des débris est constituée de déchets métaboliques des poissons et d'aliments non mangés. La taille du poisson, la température de l'eau et les pratiques d'élevage (composition des aliments, ration alimentaire et méthodes de nourrissage) comptent parmi les facteurs qui agissent sur la production de débris organiques. La plus grave inquiétude que posent ces débris au plan de l'environnement, c'est qu'ils déclenchent des poussées planctoniques locales et des conditions hypoxiques dans l'eau et les sédiments sous les cages. La compétition pour des ressources limitées et la prédation exercées par les évadés nuisent en particulier aux poissons dulcicoles indigènes.

Les déchets solides sont constitués principalement de matières fécales, les résidus d'aliments n'en constituant qu'une faible partie (Ackefors et Enell, 1990). La production de matières fécales, qui est difficile à estimer précisément, varie entre 15 à 30 % du volume d'aliments offert (Costello et al., 1996; Cho et Bureau, 2001; Bureau et al., 2003). Selon des estimations, le volume de résidus d'aliments, qui est rarement signalé, constitue entre 3 à 40 % du volume d'aliments offert (Weston et al., 1996), alors que des rapports anecdotiques et des valeurs modélisées suggèrent que le volume de résidus d'aliments issus des fermes canadiennes se chiffre actuellement à environ 5 % du volume offert. Il existe des lacunes dans les données sur les résidus d'aliments. Les déchets solides sédimentent au fond des lacs; le biote les consomme (Johansson et al., 1998) ou ils se décomposent. La plus forte accumulation se produit

directement sous les cages (Enell et Lof, 1983a), ce qui donne à penser que les effets directs sur les sédiments peuvent être limités au plan géographique. Les sédiments sous les cages subissent généralement un enrichissement en phosphore, en azote, en carbone organique et en zinc (Cornel et Whoriskey, 1993; Kelly, 1993; MacIsaac et Stockner, 1995; Troell et Berg, 1997). Bien que de nombreuses études sur les effets benthiques de la mariculture aient été publiées, peu de publications récentes documentent les effets benthiques de l'aquaculture d'eau douce. Peu d'études canadiennes sur le sujet évaluées par les pairs ont été publiées pendant la dernière décennie. Les effets des déchets de piscicultures peuvent être semblables à ceux résultant d'autres formes d'enrichissement organique, notamment une diversité réduite des espèces, une abondance accrue d'organismes résistants à la sédimentation et à une faible teneur en oxygène et une plus forte dominance de ceux-ci (Hynes, 1963; Johnson et al., 1993). En général, les effets sur les sédiments et la communauté benthique sont limités aux aires situées directement sous les cages et à proximité. Aucune étude n'a été publiée sur le rétablissement des sédiments et la reconstitution du biote des sédiments à d'anciens sites piscicoles au Canada. Plus de trois ans après l'arrêt des activités aquacoles dans des lacs d'eau douce de l'Écosse, d'importantes perturbations des communautés benthiques présentes sous les cages étaient encore apparentes (Doughty et McPhail, 1995). Les systèmes lotiques se rétablissent généralement plus vite que les systèmes lentiques en raison de la dispersion plus rapide des déchets par les courants et la reconstitution relativement rapide de la faune invertébrée (Doughty et McPhail, 1995).

Du carbone dissous, de l'azote et du phosphore sont relâchés dans la colonne d'eau par suite de leur solubilisation des aliments et des matières fécales et de l'excrétion par les poissons des produits de la respiration et d'urine (Bureau et Cho, 1999). Pour chaque tonne métrique de poissons produite, environ 3 à 10 kg de phosphore et de 39 à 55 kg d'azote sont libérés dans le milieu (Ackefors et Enell, 1994; Cho et al., 1994; Bureau et al., 2003). La plus grande partie du phosphore des déchets aquacoles se perd dans les sédiments sous forme de solides (Enell et Ackefors, 1991; Phillips et al., 1993). Les déchets azotés, en particulier l'ammoniac et l'urée, constituent la plus grande partie de la fraction des déchets dissous. En général, les augmentations décelables des teneurs en ammonium ou en ammoniac dans la colonne d'eau se produisent à proximité des cages (NCC, 1990) et dans le milieu récepteur en aval des installations terrestres (Selong et Helfrich, 1998). Aucun rapport de teneurs supérieures à celles prescrites dans les lignes directrices relatives à la qualité des eaux au niveau local ou de teneurs résultant en des eaux toxiques n'a été publié, alors que les teneurs en aval d'installations terrestres reviennent à leur niveau naturel à une distance de 400 m à 12 km des cages (Selong et Helfrich, 1998). Les élevages en cages situés dans des bassins peu profonds ou des bassins à faible action de chasse d'eau ont souvent signalé une augmentation décelable des teneurs en phosphore total, alors que les fermes situées en eau profonde où l'action de chasse d'eau est adéquate rapportent généralement qu'aucun changement décelable n'a été noté. Plusieurs études font état de teneurs élevées en phosphate dans le milieu récepteur d'effluents de fermes terrestres (Munro et al., 1985; Trojanowski, 1990). La décomposition des dépôts de déchets solides résulte en la libération de P labile dans la colonne d'eau (Kelly, 1992; Kelly, 1993). Durant les périodes de stratification, le phosphore libéré des sédiments dans des eaux hypolimniques ne sera pas disponible pour la production primaire. Peu de recherches ont été menées sur le cycle du P entre les dépôts de déchets aquacoles et la colonne d'eau, et la proportion de ce P qui sera éventuellement disponible pour la production primaire est inconnue. Ces connaissances seraient d'une grande aide dans la gestion durable de l'industrie.

La décomposition des déchets peut résulter en de faibles teneurs en oxygène dissous (hypoxie) dans les sédiments et la colonne d'eau (Axler et al., 1998), mais cet effet a rarement été signalé. La respiration des poissons d'élevage peut donner lieu à une réduction locale de la teneur en oxygène dissous. Les rapports d'une baisse de la teneur en oxygène dissous à proximité des cages varient, mais, dans l'ensemble, les sites connaissant un échange d'eau adéquat affichent une baisse de faible ampleur et de courte durée (Weston et al., 1996; Demir et al., 2001; Veenstra et al., 2003). Dans la dernière décennie, une seule étude primaire fait état de données limitées sur des profils d'oxygène dissous à des fermes canadiennes d'élevage de poissons en cages (Hamblin et Gale, 2002); il est impératif que de telles données soient recueillies et rassemblées. La demande biologique et chimique en oxygène dissous des déchets issus d'installations aquacoles terrestres peut mener à une réduction des teneurs en oxygène dissous dans les milieux lotiques sur de courtes distances en aval, mais aucune donnée récente n'a été recueillie au Canada.

L'azote, le phosphore et le carbone organique provenant des déchets métaboliques dissous et du lessivage des matières fécales et des résidus d'aliments peuvent mener à la stimulation des populations bactériennes pélagiques. La seule étude des effets sur les communautés microbiennes pélagiques fait état d'aucune augmentation de l'abondance des bactéries à proximité de cages en Colombie-Britannique, mais d'une production significativement plus élevée (MacIsaac et Stockner, 1995). Une stimulation de l'activité microbienne a été observée dans un milieu lotique récepteur d'effluents aquacoles. Par exemple, dans une rivière de la Nouvelle-Angleterre, l'abondance des bactéries et l'activité hétérotrophe dans les eaux et les sédiments en aval des points de rejet d'effluents aquacoles étaient nettement plus élevées en comparaison des sites témoins (Carr et Goulder, 1990a).

Jusqu'ici, les études de lacs canadiens n'ont pas révélé de différences dans les concentrations de chlorophylle a *entre les sites témoins et les sites aquacoles (Cornel et Whoriskey, 1993); seuls des effets localisés sur les algues périphytiques ont été signalés (MacIsaac et Stockner, 1995). En plus de stimuler la production de populations bactériennes, les substances nutritives issues d'installations aquacoles peuvent entraîner un accroissement de la production primaire (Kelly, 1993). En Finlande, les effluents aquacoles déversés dans un lac ont donné lieu à une forte augmentation de la concentration de chlorophylle* a *et de la production primaire, ainsi qu'à des changements dans la composition des espèces de phytoplancton (Eloranta et Palomaki, 1986). Dans les rivières, les effluents des installations terrestres peuvent stimuler la production primaire (Carr et Goulder, 1990b). Par exemple, Munro et al. (1985) font état d'une importante augmentation de la biomasse d'algues épilithiques et de la concentration de chlorophylle* a, *ainsi que de changements dans la composition des espèces d'algues en aval des écloseries dans plusieurs cours d'eau de la Colombie-Britannique.*

Aucune étude n'a été publiée sur les effets de l'élevage de poissons dulcicoles en cages sur les communautés de poissons indigènes au Canada. Les incidences potentielles des activités d'élevage en cages sur les communautés de poissons indigènes incluent des perturbations trophiques et des interactions entre ceux-ci et les poissons d'élevage. Au Canada, l'aquaculture d'eau douce en cages est généralement pratiquée dans des systèmes oligotrophes. L'enrichissement de ces systèmes en matières nutritives peut mener à une plus forte croissance des poissons indigènes et des poissons d'élevage qui s'y trouvent (Stockner et MacIsaac, 1996). D'autres changements trophiques peuvent se produire chez les communautés de poisons indigènes par suite de la consommation de déchets d'aliments et de matières fécales. La *consommation de déchets par le biote peut réduire les effets localisés de leur accumulation sous les enclos, mais personne n'a quantifié ce processus dans les écosystèmes canadiens.*

Il est inévitable qu'un faible nombre des poissons élevés en cages s'évadent, même en l'absence d'une défaillance totale de l'enceinte de confinement. Les dommages causés par une tempête ou l'impact d'un bateau, les attaques de prédateurs, le vandalisme et les pertes accidentelles reliées à la manipulation des poissons s'inscrivent parmi les causes d'évasion. Aucune estimation du nombre de poissons dulcicoles qui se sont évadés de leurs cages au Canada n'a été publiée. Selon des études menées à l'étranger, les évadés représentent de 3 à 5 % environ de la production totale en cages dans un plan d'eau douce donné (Phillips et al., 1985b). La prédation et la compétition pour des ressources limitées sont les principaux processus par lesquels les évadés peuvent transformer la communauté de poissons indigènes. L'introduction d'une nouvelle espèce dans un écosystème, ou une plus forte abondance d'individus d'une espèce déjà présente, donne lieu à une certaine redistribution des ressources dans la communauté ichtyenne. Les caractéristiques qui favorisent certaines espèces pour l'aquaculture sont les mêmes que celles qui peuvent leur permettre de prospérer lorsque introduites dans un plan d'eau d'où elles étaient absentes (c'est-à-dire que ce sont des espèces généralistes montrant une grande tolérance au milieu). Aucune étude n'a toutefois été publiée sur la survie des évadés dans les écosystèmes d'eau douce de l'Amérique du Nord.

Les interactions interspécifiques, en particulier celles résultant de l'établissement d'espèces introduites qui deviennent autonomes ou de la modification d'un fonds génétique indigène, sont des incidences potentiellement nuisibles de l'aquaculture. L'évasion de salmonidés d'élevage n'équivaut pas forcément à l'introduction intentionnelle de la même espèce à des fins de gestion. Les agences responsables de programmes d'empoissonnement peuvent avoir des critères de sélection différents et par conséquent préférer des stocks de géniteurs différents de ceux choisis pour l'élevage. Les traits sélectionnés pour les programmes d'aquaculture diffèrent significativement de ceux requis pour la survie dans le milieu sauvage (Bridger et Garber, 2002) et la disparité de comportement entre les sujets indigènes et les sujets domestiqués augmente en fonction de la période de captivité. Les interactions entre les évadés et les sujets sauvages peuvent être très différentes des interactions entre les poissons indigènes et les poissons ensemencés qui, après s'être évadés, ont établi des populations autonomes, selon le niveau de sélection qui s'est produit chez le stock de géniteurs. L'ampleur de tout effet permanent d'évadés d'une espèce donnée dépend du succès de leur accouplement dans le milieu sauvage avec des individus d'élevage, d'écloserie ou indigènes de la même espèce ou de l'hybridation avec des espèces étroitement apparentées. Le croisement de sujets d'élevage et de sujets sauvages ou de sujets d'élevage et de sujets ensemencés naturalisés peut produire chez ces populations des changements génétiques nuisibles à long terme (McGinnity et al., 1997; Fleming et al., 2000).

LACUNES DANS LES CONNAISSANCES ET PRIORITÉS DE LA RECHERCHE

Les incidences environnementales de la mariculture sont assez bien documentées. Par contre, peu de recherches sur les incidences environnementales de l'aquaculture d'eau douce sur les écosystèmes ont été menées au Canada, et encore moins ailleurs. Des recherches doivent être menées sur les sujets suivants.

- *Il faut connaître les facteurs qui déterminent la quantité de déchets qui s'accumulent sur le fond ou le devenir des dépôts de fond dans les écosystèmes d'eau douce. En appui de ces recherches, il faut recueillir de l'information sur les volumes courants de déchets d'aliments et les indices de consommation à des installations d'élevage commercial de poissons dulcicoles au Canada.*
- *Il faut déterminer les effets des activités aquacoles en eau douce sur les habitats et les communautés benthiques. Il faut également mener des recherches pour dégager la relation entre le volume des dépôts de déchets et la gravité des effets sur les communautés benthiques.*
- *Il faut mener des recherches sur le rétablissement des sédiments et la reconstitution du biote des sédiments après l'arrêt des activités de pisciculture en eau douce.*
- *Il faut mener des recherches dans le but de comprendre le cycle du phosphore, de l'azote et du carbone issus d'installations aquacoles en eau douce afin de pouvoir établir les conséquences écologiques de ces apports.*
- *Il faut connaître les effets des déchets de l'aquaculture sur la composition des espèces, ainsi que sur la biomasse et la productivité des producteurs primaires, des communautés microbiennes, du zooplancton et des populations de poissons indigènes.*
- *Il faut déterminer le rôle des poissons indigènes (et des évadés) dans l'exportation et la dispersion du phosphore par suite de la consommation de déchets d'aliments et de matières fécales. Cette information ajoutera à la capacité d'estimer la proportion de phosphore des déchets remis en circulation et agissant sur la production primaire.*
- *Il faut connaître les effets de tous les stades du cycle de vie des évadés sur les écosystèmes aquatiques du Canada. À cette fin, il faut documenter précisément le nombre d'évadés qui s'introduisent dans les systèmes d'eau douce et déterminer l'ampleur et le résultat des interactions écologiques et génétiques entre les poissons sauvages, les poissons ensemencés et les poissons d'élevage.*

INTRODUCTION

Rainbow trout (*Oncorhynchus mykiss*) is the most common fish species cultured in Canadian freshwater aquaculture. Other species include brook trout (*Salvelinus fontinalis*), brown trout (*Salmo trutta*), smallmouth bass (*Micropterus dolomieui)*, largemouth bass (*Micropterus salmoides*), yellow perch (*Perca flavescens*), grass carp (*Ctenopharyngodon idella*), American eel (*Anguilla rostrata*), tilapia, and Arctic char (*Salvelinus alpinus*). Cultured freshwater fish are used for a variety of purposes, including fishery enhancement, smolt production for marine aquaculture, fee-fishing, and meat fish for markets in Canada and the United States. Land-based recirculating and flow-through culture systems, the most common form of freshwater aquaculture, occur across Canada. Cage culture occurs in Newfoundland, Prince Edward Island, Ontario, Saskatchewan, and British Columbia. In the Yukon Territory, naturally fishless pothole lakes are used to culture Arctic char.

Worldwide, aquaculture operations have been linked to nutrient enrichment and eutrophication, to localized alteration or destruction of benthic habitats, and to damage to wild fish populations (Gowen et al. 1991; Gross 1998). A sound scientific understanding of how aquaculture affects the freshwater environment is required if the industry is to grow in an environmentally sustainable fashion. The purpose of this document is to provide an overview of the current state of scientific knowledge regarding the environmental effects of aquaculture activities on Canadian freshwater ecosystems and to identify areas that require further research. Emphasis has been placed on information from North American ecosystems. Where information is lacking, we have included world literature with an emphasis on European studies. However, it is important to note that differences in the habitat and species composition of European ecosystems may reduce the relevance of this literature to the Canadian experience. To ensure the scientific quality of information, we have restricted this review, with few exceptions, to peer-reviewed publications in the primary scientific literature. Changing husbandry practices, particularly developments in feed formulations (NCC 1990; Carlsson 1991), have reduced the relevance of older literature. Therefore, where possible, emphasis has been placed on literature published since 1990.

The environmental effects of cage aquaculture are complex (Figure 1) and will depend on the annual production of the farm (and therefore waste loading), husbandry practices, lake morphometry, and lake residence time (Håkanson and Carlsson 1998; Håkanson et al. 1998). Effects are largely related to two issues: (1) the production and release of waste materials, and (2) the effects of cultured fish on wild species.

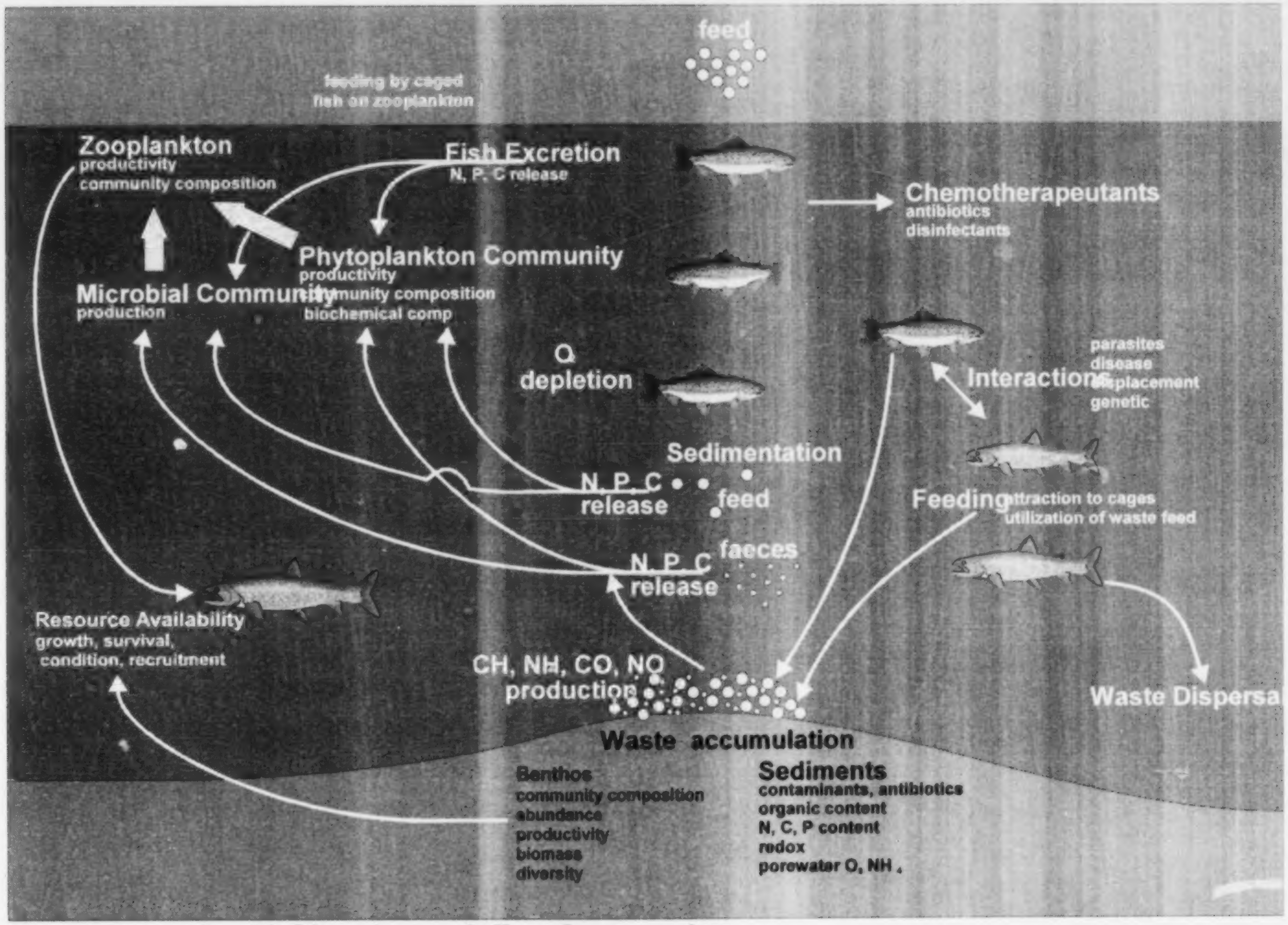
feed
feeding by caged
fish on zooplankton
Zooplankton
productivity
community composition
Fish Excretion
N, P, C release
Chemotherapeutants
antibiotics
disinfectants
Phytoplankton Community
productivity
community composition
biochemical comp
Microbial Community
production
O
depletion
parasites
disease
displacement
genetic
Interactions
Sedimentation
N, P, C
release
feed
Feeding
attraction to cages
utilization of waste feed
faeces
N, P, C
release
Resource Availability
growth, survival,
condition, recruitment
CH, NH, CO, NO
production
Waste Dispersa
Waste accumulation
Benthos
community composition
abundance
productivity
biomass
diversity
Sediments
contaminants, antibiotics
organic content
N, C, P content
redox
porewater O, NH

Figure 1. Conceptual model of the environmental effects of cage aquaculture.

WASTE PRODUCTION

Nutrient-induced stimulation of local algal blooms (eutrophication) and the creation of anoxia in waters and in sediments underlying the net pens are the primary environmental concerns associated with waste generation (Gowen 1994). There have been considerable efforts to understand the factors affecting waste production in aquaculture operations (e.g. Alsted 1991; Cho et al. 1991; Cho et al. 1994; Frier et al. 1995; Cho and Bureau 1997). Literature estimates suggest that between 5 and 10 kg of phosphorus and 39 and 55 kg of nitrogen are released to the environment for every metric ton of fish that is produced in freshwater aquaculture (Ackefors and Enell 1994; Cho et al. 1994; Bureau et al. 2003). Fish faeces and dissolved metabolic wastes comprise the majority of these wastes (Beveridge 1984). Factors affecting waste production include fish size, water temperature, and husbandry (ration, feeding method, diet composition). There is an inverse relationship between fish size and weight-specific waste production (Clark et al. 1985) and feed-conversion ratios (FCR) and thus rates of waste production may be higher in winter months (Costello et al. 1996). The factors with the greatest influence on waste production are those associated with husbandry, such as diet and feed ration.

Feed composition, including protein content and source, lipid content, and phosphorus content can have significant effects on waste production (Cho et al. 1994; Bergheim and Sveier 1995; Cho and Bureau 1997). Improvements in feeding schedules and techniques, feed digestibility, and a closer match between feed composition and nutritional requirements of cultured fish have significantly reduced FCRs and therefore waste production (Ackefors and Enell 1994; Cho and Bureau 1997). New diet formulations to reduce phosphorus (Jacobsen and Borresen 1995; Lanari et al. 1995) or to improve nutritional quality have been developed based on current nutritional information and models of fish assimilation (Cho et al. 1994; Cho and Bureau 1997; Azevedo et al. 1998; Cho and Bureau 1998). The overall goal is to produce a feed so well suited to the nutritional needs of the fish that maximum growth can be achieved with minimum waste, particularly phosphorus and nitrogen (Cho et al. 1991). Highly digestible and nutrient-dense diets for salmonids, for example, can result in outputs of less than 150 kg of solids and 5 to 8 kg of phosphorus per metric ton of rainbow trout produced (Cho and Bureau 1997). These feeds, however, are still experimental and are not currently in use by commercial aquaculture operations; never the less, over the past decade FCRs have decreased substantially. Cornel and Whoriskey (1993) reported a FCR of 3.7 at a rainbow trout farm in Quebec in the early 1990s. At that time, FCRs at Scottish farms were already down to approximately 1.2 (NCC 1990). Anecdotal and unpublished reports suggest that current FCRs are approximately 1 at Canadian land-based farms and approximately 1.2 at cage farms. Updated measurements of feed-conversion ratios and estimates of waste feed in Canadian commercial settings are a data gap and this knowledge is essential for predicting the potential effects of proposed aquaculture operations.

SOLID WASTES

Settleable solids form the major component of aquaculture waste (Merican and Phillips 1985; Ackefors and Enell 1990) and are largely in the form of faeces, but also include a small amount of waste feed, scales, mucus, and other materials. Phillips et al. (1985a) estimated that 150 to 300 kg waste feed and 250 to 300 kg of solid wastes (dry weight) are generated for every metric ton of fish produced at a rainbow trout cage farm. This solid waste production estimate is similar to a more recent estimate by Bureau et al. (2003), who reported that between 240 and 318 kg of solid wastes were produced for every metric ton of rainbow trout produced at two Ontario cage culture operations. Faecal production is estimated to range from 10% to 30% of feed (Costello et al. 1996; Bureau et al. 2003), and is affected by fish size, fish species, temperature, feed ration, and feed composition (Clark et al. 1985; Cho et al. 1994; Azevedo et al. 1998). Published estimates of waste feed range between 3% and 40% of the applied feed (Cho et al. 1994; Weston et al. 1996). Waste feed includes both uneaten feed pellets and fines, which are small particles of feed normally present in commercial feed. Fines comprise between 1% and 4% of feed and, because they are too small to be eaten by fish, directly enter the waste stream (Clark et al. 1985). The amount of waste feed is also dependent on husbandry practices such as feed type and application method (Persson 1988; Talbot and Hole 1994). It is generally believed that current levels of waste feed are under 5%, but there are no published quantifications of waste feed from North American commercial farms. Given that feed conversion ratios (calculated as dry wt. of feed applied/wet wt. fish produced) currently approach a value of 1 and that waste feed estimates are believed to be less than 5%, older estimates of total waste feed such as those reported by Phillips et al. (1985a) appear unrealistically high for current fish culture operations. Feed generally represents one of the largest expenses for a farm (Anon 1990) and therefore efforts are made to keep waste feed to a minimum.

Commercial feed typically contains from 0.7% to 1.5% phosphorus (P) and 6% to 8% nitrogen (N) (Foy and Rosell 1991a,b; Weston et al. 1996; Axler et al. 1997; Troell and Berg 1997). Phosphorus is present in excess of metabolic requirements and, if plant proteins are present in the feed, then a portion of the P is present as relatively unavailable phytate or phytin (Riche and Brown 1996). Estimates of P and N retention range from 25% to 50% and 25% to 40%, respectively (Kibria et al. 1997; Azevedo et al. 1998). Therefore, a substantial portion of these nutrients will be lost to the environment. The majority of waste P is lost to the environment in particulate matter (Ackefors and Enell 1990; Enell and Ackefors 1991), while little waste N appears in particulate form. It is estimated that over 70% of nitrogenous wastes are in the form of dissolved ammonia in fish gill and urinary excretions (Ackefors and Enell 1990; Enell and Ackefors 1991; Enell 1995).

Solid wastes from cage-culture settle and may form accumulations on the lake sediments in the vicinity of fish-pens. Sedimentation rates between 5 and 200 times background levels have been reported in lakes with cage culture operations (Enell and Lof 1983a; Merican and Phillips 1985; Troell and Berg 1997). High variability in sedimentation rates in waters surrounding net pens is typical. For example, Troell and Berg (1997) reported that sedimentation rates near net pens ranged from 17 to 296 g $dw \cdot m^{-2} \cdot d^{-1}$. There are no published data regarding sedimentation rates or benthic accumulations at Canadian farms. However, in Swedish lakes, it was observed that waste accumulations were typically localized around farms. The greatest accumulations were found directly under cages with lesser amounts extending to 25 m from the facility (Enell and Lof 1983a). The accumulation of material will depend upon current speed, the rate at which material is processed by decomposers, and also consumption by indigenous organisms (Troell and Berg 1997). Faecal material and waste feed may also be ingested by wild fish species and other biota, which can act as a mechanism for widespread dispersion of this material (Borum et al. 1995; Håkanson et al. 1998; Johansson et al. 1998). Currently, there is no published information on feeding behavior of native biota on wastes at Canadian aquaculture facilities.

Effective treatment systems for cage culture wastes have not yet been developed (Kelly 1992). Settling wastes from cage culture can be collected through the use of collecting bags or tarpaulins under the pens. This method is inefficient and rarely used, but further development is ongoing. Bergheim et al. (1991), Behmer et al. (1993), and Temporetti et al. (2000) have evaluated the use of cone-bottom collectors underneath cages for the removal of wastes from salmonid culture. Reported waste collection efficiencies in these studies have ranged from 2.5% to 16.3% (dry weight). Water movement and frequency of pumping significantly influence the efficacy of this method. Behmer et al. (1993) reported that in calm water, with daily pumping of wastes, an average of 16.3% of solid wastes was removed, but that efficiency dropped to 3.6% when the cages were subject to strong water currents. If wastes are not frequently pumped from the collectors, there can be significant solubilization of nutrients into the water column (Temporetti et al. 2000). There are ongoing trials of treatment systems in Canada, but published observations are not available.

Effluent from land-based facilities can undergo a variety of treatments before release to receiving waters, and its composition will vary accordingly. Some facilities release untreated effluent. Others may pass wastewater through settling areas and/or filtration systems before effluent release. The separated solids are collected as sludge, and therefore this fraction of the wastes does not enter the aquatic environment. As a result, wastes discharged from land-based facilities can have a greater portion of nutrients in the dissolved form. Kelly et al. (1997) reported that during normal operations, nutrients in the effluent from two Scottish freshwater salmon hatcheries were predominantly in the dissolved form. During tank cleaning however, approximately 66% of P in the effluent was in the form of particles larger than 60μ. Axler et al. (1997) examined the effluents from two Minnesota rainbow trout farms and reported that dissolved fraction of P ranged from 34% to 88% of the total P that was released. It is impossible to draw any conclusions about waste levels from the Canadian land-based industry because there is currently no compilation of data regarding the number of facilities, the level of treatment applied to wastes before disposal, waste composition, or annual waste loadings.

DISSOLVED WASTES

Dissolved carbon, nitrogen, and phosphorus are released to surface waters through the gill and urinary excretions from the cultured fish and by solubilization of faeces and feed (Bureau and Cho 1999). Dissolved nutrients are released in the gill and urinary excretions of cultured fish, are leached from faeces and feed and as they fall through the water column, and are released from the sediments as solid wastes deposited under the cages decompose (Kaushik and Cowey 1991; Kelly 1992, 1993; Bureau and Cho 1999). The nutrient content of feed, life stage of fish, fish species and water temperature all affect the production of dissolved nutrients (Kaushik and Cowey 1991; Azevedo et al. 1998; Medale et al. 1998).

Nitrogenous wastes form the largest component of the dissolved waste fraction (Foy and Rosell 1991a,b; Watanabe and Ohta 1995; Kibria et al. 1997; Azevedo et al. 1998; Naylor et al. 1999). Ammonia and urea are the primary nitrogenous wastes associated with aquaculture (Pettersson 1988). They are the metabolic byproducts of amino acid metabolism (Weston et al. 1996) and are released through gills and through fish urine. Ammonia production by fish is affected by feed composition, water temperature, and individual fish size (Cai and Summerfelt 1992; Heinen et al. 1996; Medale et al. 1998). Peak production at aquaculture sites occurs during periods of warmer water temperatures and high feeding rates (Kelly et al. 1994). Ammonia is also the primary nitrogenous release resulting from the decomposition of organic matter by heterotrophic bacteria (Wetzel 2001). Release of ammonia from waste material is slow initially, but increases with time and is temperature dependent (Pettersson 1988; Kibria et al. 1997).

Sources of dissolved P include solubilization from feed and faeces, release from accumulated waste on sediments, and the urinary excretions of cultured fish (Kelly 1992, 1993; Azevedo et al. 1998; Bureau and Cho 1999). Garcia-Ruiz and Hall (1996) estimated the fraction of total P in feed that is labile, or readily available for uptake by primary producers, to be 24%. As feed pellets sink through the water column, some of the labile P leaches from the pellets. Phosphorus leaching over a 30 m water column was estimated to be between 6% and 12% of the total P content (Garcia-Ruiz and Hall 1996). Garcia-Ruiz and Hall (1996) estimated that P solubilization from waste feed would be equivalent to only 0.3% of the soluble P excreted by cultured fish based on a waste feed rate of 20%. Twenty percent represents an extremely high rate of feed wastage. Therefore, P leaching from waste feed likely represents an insignificant source of labile P to the water column relative to leaching from faeces. Faeces have a greater proportion of labile P compared with fish feed; labile P increased from 24% of total P in feed to 43% of total P content in faeces (Garcia-Ruiz and Hall 1996). Reported rates of leaching of P from faeces were higher than rates reported for feed pellets, ranging from 54 to 251 µg P/g dw/min, and varied as a function of diet formulation (Phillips et al. 1993). Faeces sink more slowly than pellets and break apart easily, resulting in more variable leaching (Phillips et al. 1993). Phosphorus leaching from feed and faeces is estimated to account for only 10% of the overall P load to the water column (Phillips et al. 1993).

Dissolved P excretion by fish occurs primarily in the urine and is controlled by plasma phosphate concentrations (Cho and Bureau 2001). Fish receiving feed that contains a digestible P content that is closely matched to dietary requirements will excrete only minute quantities of dissolved P (Cho and Bureau 2001). Additionally, has been suggested that high levels of free alkaline phosphatase are released directly by fish (Carr and Goulder 1990a; Massik and Costello 1995). Free alkaline phosphatase could transform organic P from the fish farm effluent, as well as naturally occurring forms of organic P, into labile, dissolved reactive P that would be readily available to support enhanced primary production (Carr and Goulder 1990a). This area requires further research.

The majority of waste P is lost in the form of solid wastes (Ackefors and Enell 1990; Enell and Ackefors 1991), and the degradation of solid waste accumulations can result in the release of labile P to the water column (Kelly 1992, 1993). Troell and Berg (1997) reported a flux rate of 4 $mg{\cdot}m^{-2}{\cdot}day^{-1}$ phosphate from tropical lake sediments. In southern Sweden, Enell and Lof (1983b) reported that anaerobic sediments under farms showed phosphate release rates 30 to 550 times that of control sediments. These observations are similar to the measured phosphate flux of 0.9 to 57 $mg{\cdot}m^{-2}{\cdot}day^{-1}$ reported by Kelly (1993) from aerobic sediments collected underneath three Scottish fish farms. Enell (1983) estimated that the proportion of P from farm wastes that could be recycled back into the water column ranged between 7% and 64%. However, the factors affecting the rate and total proportion of P that is recycled from farm wastes into the water column have not been studied in any detail. In general, the release of dissolved nutrients from sediments is related to oxygen concentrations, elemental composition of the sediment ($CaCO_3$, Fe), pH, and also to bioturbation, respiration, and excretion by benthic invertebrates (Gallepp 1979; Granéli 1979; Gardner et al. 1981; Wisniewski and Planter 1987; Andersson et al. 1988; Burley et al. 2001; Gonsiorczyk et al. 2001). Phosphorus released from sediments into hypolimnetic water will not be available for primary production during periods of stratification, and the proportion of P from solid wastes that is eventually available for primary production is unknown. Because P is the nutrient limiting primary production in many freshwaters, and because the solid waste fraction is the largest component of P lost to the environment, this knowledge gap significantly hinders our ability to predict the effects of aquaculture activities on lake productivity. The cycling of P from wastes generated by aquaculture facilities and the relative importance of pathways in ecosystem cycling requires further research. Figure 2 shows the main components of the phosphorus and nitrogen budgets for a rainbow trout cage farm and available published quantifications of those components.

EFFECTS OF WASTES

DISSOLVED OXYGEN CONCENTRATIONS

Respiration by cultured fish and the biological and chemical degradation of waste materials consume water-column dissolved oxygen. In addition, indirect effects on oxygen consumption may occur due to nutrient-related increases in microbial, phytoplankton, and zooplankton biomass and its respiration and eventual decomposition

(Weston et al. 1996). During stratification, the hypolimnetic oxygen pool is fixed and consumption of oxygen by fish and decomposition processes can reduce this quantity (Wetzel 1983). The hypolimnion is used extensively as a thermal refuge during summer months by sport and commercial fish species (Christie and Regier 1988), and a reduction in hypolimnetic oxygen concentrations may negatively affect these populations.

Reports of the effects of cage culture on dissolved oxygen (DO) concentrations in the scientific literature are inconsistent. Typically, pre-impact data are not available and sampling is restricted to either comparisons of upstream versus downstream or control versus cage-site sampling with only temporal replication. Hypolimnetic anoxia as a result of organic enrichment from aquaculture has been reported in small, deep mine-pit lakes (Axler et al. 1996). This is the only relatively recent study that is properly replicated and uses a truly independent control site. However, the application of the results from this study to the Canadian industry is limited due to the very unique environment. Mine-pit lakes have little or no water renewal, which is not the case for most commercial cage-farm sites in Canada. One of the aquaculture-affected lakes in the study also exhibited incomplete mixing and thus limited reoxygenation of hypolimnetic water. Cornel and Whoriskey (1993) observed mid-summer oxygen depletion below 2.5 m at a farm site in Quebec. The reduction averaged 4 $mg{\cdot}L^{-1}$ and was restricted to the depths occupied by the cage. However, the FCR for this farm was 3.7, indicating a much higher waste production than currently occurs. The farm also used an airlift to bring cool, hypolimnetic water to the surface during the summer, and hypolimnetic water at all sampling stations in Lac du Passage exhibited oxygen depletion during this time. It is possible that this upward movement of hypolimnetic water in the vicinity of the cages contributed to the observed reduction in dissolved oxygen concentrations. Recently, Clerk et al. (2004) reported that paleolimnological sampling of sediments and analysis of chironomid remains suggest that hypolimnetic anoxia developed in the vicinity of a cage culture facility located in the LaCloche Channel of Lake Huron, an area of reduced flow.

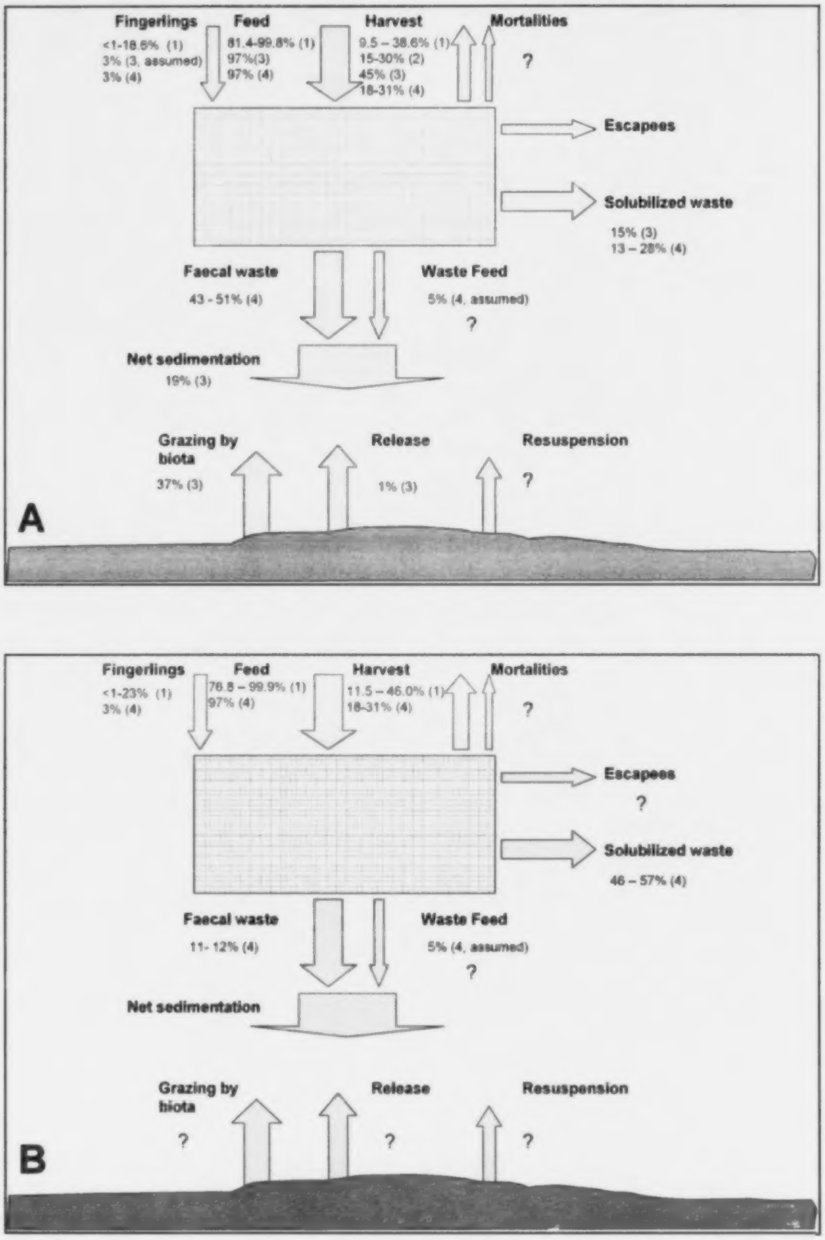
Fingerlings
<1-18.6% (1)
3% (3, assumed)
3% (4)
Feed
81.4-99.8% (1)
97%(3)
97% (4)
Harvest
9.5 – 38.6% (1)
15-30% (2)
45% (3)
18-31% (4)
Mortalities
?
Escapees
Solubilized waste
15% (3)
13 – 28% (4)
Faecal waste
43 - 51% (4)
Waste Feed
5% (4, assumed)
?
Net sedimentation
19% (3)
Grazing by biota
37% (3)
Release
1% (3)
Resuspension
?
A
Fingerlings
<1-23% (1)
3% (4)
Feed
76.8 – 99.9% (1)
97% (4)
Harvest
11.5 – 46.0% (1)
18-31% (4)
Mortalities
?
Escapees
?
Solubilized waste
46 – 57% (4)
Faecal waste
11- 12% (4)
Waste Feed
5% (4, assumed)
?
Net sedimentation
Grazing by biota
?
Release
?
Resuspension
?
B

Figure 2. Phosphorus (A) and nitrogen (B) budgets for a freshwater cage farm with literature values, where available, for each component. Values have been expressed as % of total P or total N inputs. Numbers in brackets refer to literature source: (1) Penczak et al. 1982; (2) Håkanson et al. 1988; (3) Johansson et al. 1998; and (4) Bureau et al. 2003.

However, a recent forensic analysis of published and unpublished data regarding the LaCloche channel (Naylor 2004) has raised the possibility that reduced oxygen in the hypolimnion of this area occurred periodically prior to the start of fish culture. Minimal effects of net pen culture on DO concentrations are reported in other studies. Phillips et al. (1985b, as cited in Weston et al. 1996) reported an average reduction in DO concentrations of only 0.7 $mg \cdot L^{-1}$ measured at a distance of 150 m from cages, relative to reference sites, but this study is dated. Demir et al. (2001) reported mostly non-significant differences in the dissolved oxygen concentrations upstream versus downstream of fish cages in an oligotrophic and non-stratified reservoir. Veenstra et al. (2003) reported statistically significant reductions in DO concentrations at depths of 0.5 to 3 m during stratification in the vicinity of net pens in a reservoir in Oklahoma. During one year of the study they also detected a depletion of water column DO in the vicinity of the net pens that lasted for approximately 2 weeks following turnover. An examination of the literature leads to the conclusion that there are currently few data, at least in the primary literature, to support any clear conclusions regarding the effects of cage culture on dissolved oxygen concentrations in lakes. However, in Ontario the operators of fish farms are required to monitor and report DO concentrations, and marked reductions would result in action to reduce the farm's effect. This has happened only at the LaCloche site, suggesting that effects have not been observed. It should also be noted that the development of reduced hypolimnetic oxygen and localized anoxia above lake sediments is neither an unnatural nor rare occurrence in pristine lakes (Wetzel 2001). Siting practices that avoid placing cages in areas of poor water circulation, observe proper husbandry, and restrict farm production to levels that do not result in significant accumulation of organic wastes will reduce the probability of development of hypolimnetic hypoxia.

The discharge of wastes from land-based aquaculture facilities can affect DO concentrations in lotic (moving) waters, although data specific to Canadian ecosystems are lacking. Trojanowski (1990) reported increased 5-day biological oxygen demand (BOD_5) and chemical oxygen demand (COD) in the Lupawa River, Poland, as the result of a rainbow trout facility. The BOD_5 increased by 0.4 to 1.4 $mg \cdot L^{-1}$ and then returned to background levels several km downstream of the facility. Boaventura et al. (1997) reported DO reductions of 0.7 to 2.4 $mg \cdot L^{-1}$ downstream of three rainbow trout farms in northern Portugal. Brown and King (1995) also reported significant reductions in DO concentrations due to the BOD and COD of settling wastes, but they were limited to downstream depositional areas. Selong and Helfrich (1998) reported significant reductions in DO downstream of three of five trout farms in Virginia, USA, and indicated that reductions were greatest post-feeding and predawn. Although the reductions were statistically significant, they did not result in water column DO below 6.5 $mg \cdot L^{-1}$ at any time.

CHANGES IN WATER NUTRIENT CONCENTRATIONS

Literature reports of the effects of aquaculture on water column nutrient concentrations in lakes are inconsistent. Effects resulting from nutrient loading by fish farms will be modified by basin morphometry, flushing rate, water chemistry, biological activity within the lake, and land-use patterns in the watershed. Kelly (1995), in a survey of 6 Scottish freshwater lochs with trout culture, reported that changes in water column total phosphorus (TP) could be adequately modeled from farm feed data only in lochs that had no other significant alterations to nutrient cycling or sources within their watershed.

Reports of significant increases in nutrient concentrations as a result of cage culture are typically found in older literature (farms with high FCR), or in literature concerning fish farming in shallow basins or small basins with reduced flushing rates (e.g., Stirling and Dey 1990; Axler et al. 1996). In contrast, MacIsaac and Stockner (1995) reported no change in water column nutrients at two cage sites in British Columbia lakes; Veenstra et al. (2003) reported no significant increases in water column N or P as a result of trout cages in Lake Texoma, Oklahoma; and Demir et al. (2001) showed only small and seasonal differences in PO_4-P, NO_2-N, NO_3-N, and NH_3-N concentrations downstream of rainbow trout net pens in a Turkish reservoir. Similarly, Cornel and Whoriskey (1993) found no effect of a small cage operation on water column nutrient concentrations in Lac du Passage, Quebec, even though the FCR for the operation was high (3.7). This operation was small (14 metric tons annual production), which may be at least partially responsible for the lack of observed effect. The most recent study of a Canadian farm (Hamblin and Gale 2002) reported that total phosphorus concentrations in Lake Wolsey (Manitoulin Island, Ontario) during autumn turnover have doubled since the start of cage culture. However, this statement is based upon data from water samples collected within a 50 m radius of the cages, while spring turnover water samples collected at a "deep station" an undisclosed distance from the cage farm showed no similar increase over 13 years of production. The data presented are limited; it is difficult to determine whether they are single point measures or averages, as little information for sample size or variability is provided, and there were no data available from autumn sampling at the deep station. It possible that there is a seasonal increase in TP coinciding with the production cycle which is then flushed out during the off-season so that by spring there is no longer any observed increase. However, as measures of total phosphorus can include a significant component as particulate phosphorus, it is also possible that the observed autumn increase in TP in close vicinity of the cages reflects inclusion of particulate waste, which would be in greater abundance during that portion of the production cycle and because autumn is typically when a lot of net cleaning takes place. The limited nature of the data presented does not allow us to distinguish between these possibilities. A recent paper reporting effects on water nutrient concentrations in reservoir in Argentina is also problematic. Temporetti et al. (2001) reported that an increase in TP and dissolved inorganic nitrogen was observed at a site influenced by a fish farm. However, although the means presented are higher, the paper does not present any statistical analysis of the data to assess significance and the range of values collected both before and after fish farming show considerable overlap. At the same location, Baffico and Pedrozo (1996) reported no significant difference. In general, the reviewed literature supports the view that modern cage farms with good husbandry that are located in well-flushed, deep basins do not show significant, long-term effects on water column nutrient concentrations.

Ammonia is released directly by fish and from the decomposition of wastes. It is present in water both as the ammonium ion and as un-ionized ammonia. Un-ionized ammonia, which is the form with the greatest toxicity to aquatic life, is normally present in much smaller concentrations than ammonium, and the ratio of the two forms is dependent upon pH and water temperature (Trussell 1972; Wetzel 1984). Published acute toxicity thresholds for un-ionized ammonia range from 0.32 $mg \cdot L^{-1}$ to 0.63 $mg \cdot L^{-1}$ for rainbow trout (USEPA 1985) and from 2.0 to 2.6 $mg \cdot L^{-1}$ for the mayfly *Ephemerella grandis* (Thurston et al. 1984). It is unlikely that ammonia discharges from fish culture will result in toxicity to wild fish (NCC 1990, Weston et al. 1996). However, toxicity to benthic invertebrates inhabiting sediments directly under cages is possible and this area of research has not as yet received any attention in the published literature.

Reports of significant effects of land-based farms on the nutrient content of running waters are more consistent. In general, detectable increases in water column ammonium or ammonia concentrations are reported in receiving waters downstream of land-based facilities, but return to background levels at distances ranging from 400 m to >12 km (Kendra 1991; Boaventura et al. 1997; Selong and Helfrich 1998). The wide range in distance affected is likely due to a combination of varying size/feed use at the farms and varying effluent dilution in the receiving waters, but these data were not presented. Reported increases are small and there are no published reports of concentrations that exceed local water quality guidelines or cause toxicity. Kendra (1991) surveyed the effluents of salmonid hatcheries in Washington State and reported significant but small (0.01–0.85 $mg \cdot L^{-1}$) increases in ammonia concentrations between influent and effluent waters. Selong and Helfrich (1998) reported elevated total ammonia-N in four of five Virginia streams receiving effluent from trout farms. This increase was still detectable 400 m downstream of the discharge point, but was well below toxicity thresholds for aquatic vertebrates and invertebrates even during low flow periods. Trojanowski (1990) reported average increases of 0.04 $mg \cdot L^{-1}$ nitrate N, 0.24 $mg \cdot L^{-1}$ ammonium N, 0.033 $mg \cdot L^{-1}$ phosphate, and 0.058 to 0.068 $mg \cdot L^{-1}$ total P in the Lupawa River, Poland, as a result of trout culture. Boaventura et al. (1997) reported increases of 0.27 to 1.46 $mg \cdot L^{-1}$ ammonia and 0.060 to 0.579 $mg \cdot L^{-1}$ dissolved P in Portuguese rivers receiving effluents from trout farms. Carr and Goulder (1990b) reported detectable increases in soluble reactive P (PO_4-P) and organic P concentrations downstream of two fish farms in New England. Brown and Kings' (1995) survey of trout farms in South Africa, found that levels of nitrate, ammonia, and dissolved phosphate were significantly elevated below farms during low flow season. Similarly, Munro et al. (1985) reported elevated phosphate and ammonia concentrations in several British Columbia rivers receiving hatchery effluents.

MICROBIAL COMMUNITIES

Nitrogen, phosphorus, and organic carbon leaching from feed pellets and from fish faeces may stimulate production in pelagic bacterial populations. MacIsaac and Stockner (1995), the only study in which effects on pelagic microbial communities has been investigated, reported no difference in abundance, but significantly higher production of bacteria near net pens in a lake in British Columbia. Production rates during August at net pen sites were nearly double those at control sites. There was a similar increase in the production of heterotrophic nanoflagellates, protozoans that feed on bacteria and, in turn, serve as a food source for mixotrophic phytoplankton and zooplankton. In addition to serving as a food resource for higher trophic levels, pelagic bacteria can play an important role in the recycling of P within the epilimnion (Wetzel 2001). Clearly, the effect of fish farm emissions on the pelagic microbial community and resulting implications to the rest of the food web is an area requiring further research.

Microbial stimulation is also observed in lotic water receiving fish farm effluents. Carr and Goulder (1990a) reported a significant increase in bacteria abundance and heterotrophic activity in river water and sediments downstream of fish farm effluent outfalls in New England. They also reported an increase in extracellular alkaline phosphatase activity (APA). Increases in bacterial abundance and APA downstream of fish hatcheries have also been reported by Baldock and Sleigh (1988). APA is correlated with bacterial abundance and is generally considered a reflection of microbial activity or of algal P deficiency (Smith 1995; Wetzel 2001). Extracellular AP can also be a product of animal excretion, leading Carr and Goulder (1990a) and Massik and Costello (1995) to suggest that high levels of free alkaline phosphatase are released directly by feeding fish. Free alkaline phosphatase carried downstream of a fish farm could transform organic P from the fish farm effluent as well as naturally-occurring forms into labile, dissolved reactive P, which would then be readily available to support enhanced primary production at some distances from the aquaculture facility (Carr and Goulder 1990a). It is important that we develop a better understanding of the magnitude and environmental significance of this release (Carr and Goulder 1990a).

PHYTOPLANKTON COMMUNITIES

There are few published studies of the effects of freshwater cage farming on phytoplankton populations and recent publications have not reported any detectable effects. Demir et al. (2001) reported no significant change in chlorophyll *a* or species composition downstream of culture pens, and Veenstra et al. (2003) could detect no significant difference in chlorophyll *a* concentrations between their control sites and a net pen operation. Cornel and Whoriskey (1993) reported no differences in chlorophyll *a* concentrations between a control site and a farm site in a lake containing a small rainbow trout cage farm in Quebec, but suggested that long-term monitoring might be more successful in detecting effects. Older literature has reported enhanced primary production rates, increased algal biomass, and changes in algal species composition (Trojanowski et al. 1985a; Kelly 1993). For example, fish farm nutrient loading resulted in significant increases in chlorophyll *a* and primary productivity, and a change in species composition of phytoplankton during the open water season in Lake Konnevesi, Finland (Eloranta and Palomaki 1986). Phytoplankton communities near the farm became dominated by *Gonyostomum semen*, a flagellate alga known to cause skin irritation in humans (Cronberg et al. 1988). Many of these observations are, however, almost 20 years old and may not be representative of present day effects.

The monitoring of algae on fixed surfaces may provide a sensitive measure of point-source nutrient-enrichment (Heinonen and Herve 1984). MacIsaac and Stockner (1985) used fixed artificial substrates to determine effects of cage emissions on periphytic algae along the shore and in the water column in a lake in British Columbia. They reported a 10-fold increase in accrual rates of periphytic algae on the artificial substrates suspended near cages. However, the effect was localized: just 150 m away only a 3-fold increase was observed. Baffico and Pedrozo (1986) also used artificial substrates to look at differences between periphyton upstream and downstream of a fish farm in an Argentine reservoir. They reported significantly higher biomass at the site affected by fish farm wastes, but did not report the distance from the cage to the substrates.

A change in the ratio of nutrient availability can also have significant effects on algal populations. Although primary productivity in most freshwaters is P-limited, other required resources, such as N and Si, may become limiting when there is sufficient P (Tilman et al. 1986; Kelly 1993). The N:P and the Si:P ratio can influence the species composition of phytoplankton (Tilman et al. 1986). Fish farm discharges often have low N:P ratios in soluble nutrients (Foy and Rosell 1991a), and N:P ratios below 20 can favor the competitive selection of N-fixing cyanobacteria (Foy and Rosell 1991a). Blooms of N-fixing cyanophytes have been observed in lakes affected by cage culture (Stirling and Dey 1990; Foy and Rosell 1991a). More recently, Baffico and Pedrozo (1996), studying the effects of rainbow trout cage farming in a reservoir in Argentina, reported a phytoplankton community dominated by diatoms, rather than the expected cyanophytes, as a result of the influence of fish farm wastes. The authors attributed this observation to a high Si:P ratio in the reservoir, which would have favored diatoms as they are more efficient at phosphorus uptake when sufficient Si is present (Tilman et al. (1986). It is also possible that the low temperatures observed in the reservoir (average 9.0–9.2°C, range 6.2–17.2°C) contributed. Tilman et al. (1986) reported that diatoms were competitively dominant over green and blue-green algae over a broad range of N:P ranges at temperatures below 14°C. There is currently no published information about the effects of cage culture operations on the species composition of phytoplankton communities or production of harmful algal blooms in North American ecosystems.

Discharges from land-based farms have been shown to affect primary producers in receiving waters (Bergheim and Selmer-Olsen 1978; Munro et al. 1985; Carr and Goulder 1990b). Munro et al. (1985) reported a significant increase in periphytic algal biomass and chlorophyll *a*, and changes in species composition downstream of hatcheries in several British Columbia streams. Selong and Helfrich (1998) reported increases up to 10-fold in periphyton chlorophyll *a* in five Virginia streams downstream of trout farms, but effects were restricted to within 400 m of the farms. In England, increased growth of periphytic algae downstream of farm discharges was observed and determined to be related to P addition (Carr and Goulder 1990b). Carr and Goulder (1990b) also observed higher tissue-P concentrations and greater adventitious root development and growth of shoots of the macrophyte *Ranunculus penicillatus*, although the authors noted that weed cutting may have confounded these observations.

It is important to note that aquaculture P wastes are largely a hypolimnetic input. Approximately 70% of P outputs are in the form of solids that quickly settle (Enell 1995). The majority of feed usage occurs during summer months and, thus, most P inputs occur to the hypolimnion during the period of thermal stratification. This prevents the movement of P into the euphotic zone and may substantially reduce the effects of P loading. Schindler et al. (1980) demonstrated that the addition of nutrients to the hypolimnion of a lake resulted in phytoplankton standing crops and productivity only 10% to 21% that of a lake fertilized in the epilimnion. Note, however, that this reduction was at least partly due to binding of P by humic materials. The environmental fate of P from freshwater aquaculture is one of the most important research needs for the future.

ZOOPLANKTON COMMUNITIES

Cage aquaculture has the potential to affect the zooplankton community through nutrient-related changes in the phytoplankton community, through changes in dissolved oxygen concentration, or through direct predation by caged fishes. The literature already reviewed suggests that the probability of such influences occurring is small and likely associated with farms that are poorly sited or managed. Although changes in phytoplankton community structure have not been detected around aquaculture sites, the literature is sparse and it is possible that nutrient release by farms may affect the productivity, nutrient status, and community composition of phytoplankton, thereby affecting both the quantity and quality of zooplankton food resources. A change in resource availability and quality may, in turn, mediate changes in zooplankton abundance and species composition. As an example, Schindler (1990) reported a decrease in zooplankton body size and lifespan (increased relative importance of r-strategists) following nutrient enrichment of a lake at the Experimental Lakes Area, Ontario. There is little published information documenting the effects of cage aquaculture on zooplankton communities. Cornel and Whoriskey (1993) observed a reduction in mid-summer density of *Daphnia* in the vicinity of a Quebec rainbow trout farm, but they could not determine whether the decline was due to predation or avoidance of the cages. Demir et al. (2001) reported increased abundance of zooplankton at a cage site in Turkey during January and April, but differences were not significant at other sampling dates. There is a gap in knowledge regarding the mechanisms through which cage aquaculture affects zooplankton communities and the collection of data to support further research in this area is suggested.

BENTHIC EFFECTS

SEDIMENT CHARACTERISTICS

Sediments under farms may accumulate quantities of faeces and waste feed, resulting in a flocculent layer high in organic content (Gowen et al. 1991). The thickness of the layer will be dependent on the assimilative capacity of the benthic community and removal of wastes by biological and hydrodynamic processes. In the North Channel of Lake Huron, accumulations under and in the vicinity of commercial cages operations are variable. Cages placed in areas with rocky bottoms and/or reduced flushing have greater accumulations than sites with higher flushing and/or soft bottoms (Murray Charlton, Environment Canada, personal communication). It is believed that this may be due to better adaptation of soft-bottomed communities to survival in and assimilation of high organic content waste materials.

Sediments beneath fish cages generally show enrichment in P, N, and organic carbon (Trojanowski et al. 1982; Enell and Lof 1983b; Korzeniewski and Moczulska 1985); (Trojanowski et al. 1985b; Trojanowski 1991; Cornel and Whoriskey 1993; Kelly 1993; Troell and Berg 1997). In a study in Lake Letowo, Poland, Trojanowski et al. (1982) reported that sediment organic content under trout cages was 25%, while the range at control sites was 5% to 10%. Total N was approximately twice as high under the cages as at control sites, while P showed only a slight increase. Elevated sediment C, N, and P were observed beneath a trout cage (40t production) in Lake Szczytno Male, Poland (Trojanowski et al. 1985b). Kelly (1993) also observed an increase in the organic content and P content of sediments relative to control sites at three Scottish freshwater trout farms. Enell and Lof (1983b) recorded increases in N and P flux, and increases in sedimentary respiration rate and pore water P concentration beneath Swedish cages. Rooney and Podemski (unpublished data) found that sediment organic content, N, P, and pore-water ammonia levels were all elevated in sediments directly below a fish farm in Ontario, but that these changes did not extend more than a few meters beyond the edge of the cage.

Aquaculture may also lead to increased concentrations of some elements, such as copper and zinc beneath fish cages. There are several reports of elevated zinc and copper in sediments beneath marine net pens (Parker and Aubé 2002; Chou et al. 2002). In these instances, the copper is believed to be associated with copper-based antifoulant coatings on the nets while the source of zinc is believed associated with mineral supplements in the feed (Chou et al. 2002). Although there are currently no primary-literature publications containing data from freshwater cage sites in Canada, elevated copper, zinc have been observed in freshwater sediments affected by fish farming (Rooney and Podemski, unpublished).

Changes to the composition of aquatic sediments are one of the more direct effects resulting from cage aquaculture. However, more information is required to understand the modifying effects of factors such as depth, bottom type, and current regime on the thickness, composition, and longevity of bottom deposits. The relationship between changes in sediment characteristics and the biotic community is also not understood, and is the focus of ongoing research.

EFFECTS ON ZOOBENTHOS

Although there is extensive literature on the benthic effects of marine aquaculture, there are few published accounts of effects at freshwater cage sites, and none are recent enough to evaluate the outcomes of current industry practices. References that exist generally provide only partial information about farm operation (production, species, feed composition, FCR), which makes determining the applicability of these studies to the current Canadian industry problematic. Many studies also do not provide sufficient data (e.g., variance estimates) to allow the calculation of effects size and thus inclusion into meta-analysis. Effects of fish farm wastes are similar to those associated with other forms of organic loading. Typically these responses include a decrease in taxa richness and diversity due to the loss of sensitive species such as mayflies (Ephemeroptera), stoneflies

(Plecoptera), and caddisflies (Trichoptera), and an increase in the abundance and dominance of organisms resistant to sedimentation and reduced oxygen availability, such as freshwater worms (Tubificidae, Oligochaeta), and some midges (Chironomidae) (Hynes 1963; Johnson et al. 1993).

Dobrowolski (1987a,b) and Doughty and McPhail (1995) both reported on the effects of cage culture on lentic (pond or lake) benthic communities. Dobrowolski et al. (1987b) found higher densities of oligochaetes and chironomids, in particular chironomids in the tribe Chironomini, in close vicinity to cages. Chironomini larvae feed on organic detritus (Zieba 1984) and typically benefit from moderate increases in organic loading. Dobrowolski et al. (1987b) reported a reduction in the abundance and diversity of Ephemeroptera, snails and bivalves (Mollusca), sand flies (Ceratopogonidae), and leeches (Hirudinea), and a reduction in the diversity of Oligochaeta near cages. Unfortunately, the applicability of these findings to Canadian aquaculture sites is limited. The trout culture facility was located over littoral sediments in less than 10 m of water, a practice that does not occur in Canada. In addition, the FCR for the farm was 2.5 (Korzeniewski and Salata 1982), indicating a substantially higher waste loading than would be expected from a Canadian cage culture facility under modern operating practices. In a review of 16 freshwater cage sites located in Scottish lochs, Doughty and McPhail (1995) reported localized effects at 6 of 10 farm sites, with oligochaete densities in the vicinity of cages two orders of magnitude greater than at control sites. Cornel and Whoriskey (1993), the only Canadian study, were unable to measure effects because no benthic invertebrates could be found below 13 m at either lake pen or control sites in the study lake. However, the mesh size employed by the researchers in this study (1 mm) was so large that the majority of profundal benthic organisms would not be captured.

Recently, paleolimnological methods have been used to examine the effects of cage culture operations on benthic chironomid communities at two Canadian farm sites. Clerk (2002) reported that fish farming activities at one site resulted in a rapid decline in the abundance of chironomid taxa that were sensitive to low oxygen and increased sedimentation, and an increase in abundance of anoxia-tolerant species. At a second site, less dramatic effects could be inferred, when only slight elevations in the abundance of taxa associated with eutrophic conditions occurred.

Effects on lotic waters are similar to those reported for lentic studies as well as those generally associated with loading of particulate organic matter (Hilsenhoff 1987; Hilsenhoff 1988). Typically, organic loading to streams results in a decrease in the abundance of the EPTs (Ephemeroptera, Plecoptera, and Trichoptera), an increase in the abundance of chironomids and oligochaetes, a decrease in species diversity and richness, and an increase in total biomass, largely of chironomids and oligochaetes. Doughty and McPhail (1995) conducted surveys of the receiving waters of 18 land-based farms in Scotland. Observed effects included increased predominance of oligochaetes and chironomids. Occasionally, benthic communities lost pollution-sensitive taxa such as mayflies (Ephemeroptera) and stoneflies (Plecoptera), but more often these taxa were still present. Munro et al. (1985) reported similar findings in British Columbia streams receiving hatchery effluents. Selong and Helfrich (1998) examined benthic communities in five Virginia streams receiving effluents from land-based trout culture. They reported a reduction in macroinvertebrate taxa richness and abundance of EPTs downstream of the farms. The abundance of pollution-tolerant taxa such as aquatic sow bugs (Isopoda) and snails (Gastropoda) increased in the downstream sites. Loch et al. (1996) reported increased abundance of oligochaetes and gastropods downstream of trout farms in North Carolina. Brown and King (1995) surveyed the receiving waters of seven trout farms in the South-West Cape, South Africa. They reported the reduction or loss of sensitive taxa including Plecoptera; leptophlebid, heptageniid and ephemerellid mayflies; and elmid aquatic beetles (Coleoptera). They also observed an increase in oligochaetes (Naididae, and Lumbiculidae), chironomids and aquatic flat worms (Planaria) downstream of farm outfalls. Camargo (1992) reported a decrease in diversity and species richness and an increase in biomass and total abundance of macroinvertebrates downstream of a trout farm in Spain. The spatial effect of farms appears to be limited, with recovery apparent 1 km downstream in some (Kendra 1991; Camargo 1992; Selong and Helfrich 1998), but not all cases (Loch et al. 1996). This variability is likely related to waste loading and dilution within the receiving water.

The published literature on the effects of aquaculture on benthic communities in both lentic and lotic freshwater ecosystems suffers from a number of deficits. In general, studies fail to provide the information about farm operations that would be required to assess comparability between studies. The majority of studies are too old to provide an assessment of modern operating practices. The sampling methods used and mesh sizes employed vary widely and are occasionally not even reported. Typically, there are no pre-operational data and studies have generally restricted sampling to a comparison of underneath cages or downstream of outfalls with distant control sites in the same body of water. Additionally, little consideration has been given to the information that could be gained by sampling along the gradient of organic "enrichment" that occurs as one moves away from the source of wastes.

Pearson and Rosenberg (1978) provided a model describing the structural changes that occur in marine benthic communities along a gradient of organic enrichment; it is not known if responses follow similar trajectories in freshwater environments as no study has thus far used a gradient sampling design. Pearson and Rosenberg's generalized SAB (species, abundance, biomass) relationships along a gradient of organic enrichment are shown in Figure 3.. In areas with considerable organic enrichment, the number of species, the abundance, and total biomass of the community will all be low; under extreme situations, macroinvertebrates may even be extirpated. As the degree of enrichment declines, total abundance will peak. This peak is composed of large numbers of very few opportunistic species that are able to colonize newly depauperate habitats and to survive under conditions typical of high organic enrichment: reduced oxygen availability, increased ammonia, and high sedimentation. After this peak, the total abundance slowly declines towards that of the unaffected community. The total number of species within the community rises more slowly along the declining enrichment gradient, and peaks within a transition zone. In this area, the number of species is greatest because the community contains both the more tolerant species from the natural community as well as species from the enrichment-tolerant community. Measures of community diversity – such as the Shannon-Weiner index (H) – will reach maximum value at the beginning of the transition zone. As the degree of organic subsidy further declines, so do the species number and diversity values as the assemblage gradually approaches the composition of an unaffected community. Changes in biomass along the organic enrichment gradient occur along a similar trajectory as species richness. Biomass of the benthic community will be quite low or entirely absent under conditions of extreme organic additions. As organic enrichment declines, community total biomass will rise slowly and peak in the transition zone in approximately the same location as the peak of species number. A secondary, smaller peak in biomass may be observed earlier along the gradient in the area in which conditions are favorable for enrichment opportunists. Weston (1990) further clarified that a pattern of reduced interspecific but increased intraspecific measures of individual biomass occurs as enrichment increases. The secondary biomass peak, termed the "peak in opportunists" by Pearson and Rosenberg (1978), occurs in the area of high intraspecific biomass of opportunistic species and may be difficult to detect as the short life-span typical of opportunists can result in high seasonal variability. Weston (1990) also indicated that methodological difficulties in adequately sampling rare and large biomass species in unaffected zones can result in skewed biomass data.

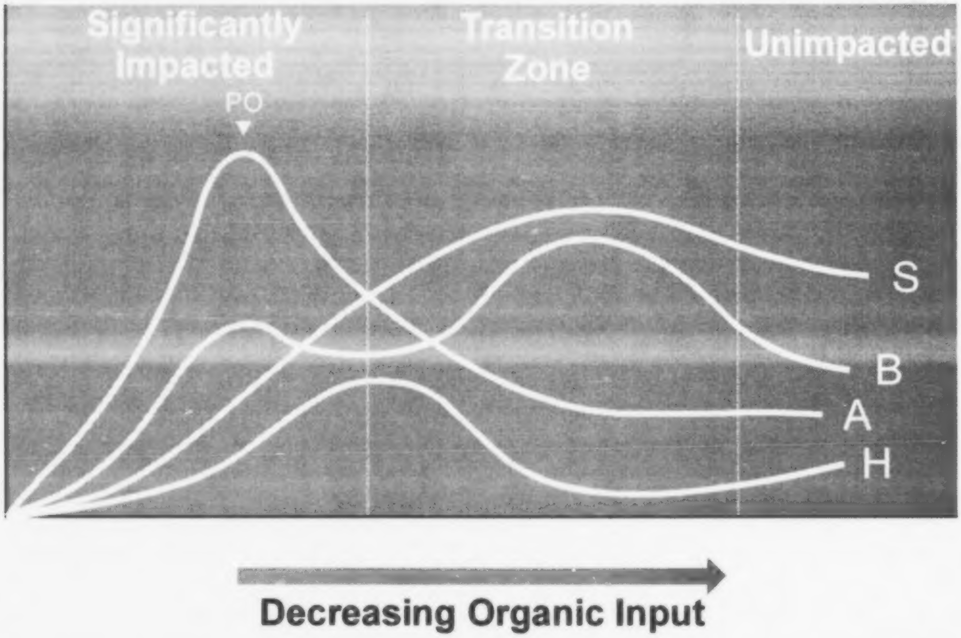

Figure 3. Species (S), abundance (A), biomass (B), and diversity (H) curves along a gradient of organic enrichment. Modified from Pearson and Rosenberg (1978).

Under-cage versus reference site sampling programs can result in apparently conflicting results if the concept of community response along a gradient of enrichment is not considered. It is important to realize that each cage site may fall in a different location along this hypothetical enrichment gradient, depending upon the farms' waste loading and the assimilative capacity of that particular environment. It is also important to realize that the successional changes in community structure occur not only along a spatial scale of organic enrichment, but also temporally after the start of an organic addition, or in reverse as recovery proceeds after organic enrichment is reduced. Once again, depending upon the duration of operation, sites with similar waste loading may fall on a different point along the gradient. When considering temporal gradients it is also important to consider that affected areas of profundal sediment are to some degree habitat "islands," and that the colonization of affected patches of sediment may be subject to the same modifying factors such as dispersal ability, size of patch, and distance from source of colonizers. Thus far, no published studies have taken a gradient approach to sampling in order to examine this relationship in freshwaters, although a study at the Experimental Lakes Area is ongoing (Rooney and Podemski, unpublished).

BENTHIC RECOVERY

Recovery of lotic systems from fish farm emissions is generally rapid due to removal of wastes by water flow and relatively swift colonization by invertebrate drift. Doughty and McPhail (1995) reported complete benthic recovery 19 months after closure of a smolt rearing operation. Lentic profundal habitats, however, contain a low biomass and diversity of organisms, and recolonization processes are likely slower. These characteristics will reduce the ability of the benthic environment to assimilate waste material from cages and may slow recovery processes relative to rates reported in marine or lotic freshwater systems. Doughty and McPhail (1995) reported that severe effects on the benthic community below a cage site were clearly apparent for more than 3 years after cessation of farming. The study of recovery and impairment to recovery of freshwater benthic habitats after aquaculture ceases are areas requiring further research. One Canadian study, ongoing at this time, is investigating recovery of sediments (but not biota) after cessation of operations at an Ontario cage farm (Murray Charlton, Environment Canada, personal communication).

FISH POPULATIONS

The primary mechanisms through which cage aquaculture has the potential to affect wild fish populations are: direct, by an energetic subsidy in the form of faecal matter and waste feed consumed by wild fish; indirect, through food web changes mediated by waste inputs to the ecosystem; and, through the ecological and genetic interactions that may occur between escapees and indigenous species. At the time of this review, there are no published studies that examine the effect of freshwater cage aquaculture operations on native fish in Canada. Because of the lack of published research on fisheries-related effects of aquaculture in Canadian freshwaters, this section will follow a format similar to previous sections by drawing upon relevant studies from other geographic areas. However, research on the effects of aquaculture in freshwaters has not kept pace with the expansion of this industry, resulting in few advances in our understanding of how current practices affect native fish populations.

A wide variety of waste recovery and treatment techniques are currently applicable to land-based culture and therefore this section will focus solely on the environmental effects of caged-farm aquaculture on native freshwater fish communities. For the purposes of this review we refer to wild or native fish as those indigenous to the system in question. Stocked fish are those added to aquatic systems from other systems or hatcheries for stock enhancement or other management objectives and may not be native to that particular ecosystem, but the purpose of their addition is to produce self-sustaining populations. Finally, we refer to farmed or escaped fish as those being raised in aquaculture facilities whose origin is from hatchery stock.

The intensive cage-culture of salmonine fish (char, salmon, trout) dominates the Canadian freshwater aquaculture industry and rainbow trout, *Oncorhynchus mykiss*, is the most commonly reared species. The effects of cage operations on wild fish populations can be split into two broad areas: (1) trophic alterations, and (2) native–farmed interactions. Our discussion of trophic alterations will include the responses of native fish to the increased nutrient concentrations and subsequent increased productivity of water bodies associated with aquaculture practices, as well as the consumption of waste feed and faeces. In the section dealing with interactions between wild and farmed fish, we identify the risks associated with the introduction of fish species through freshwater aquaculture, including behavioral interactions, disruption of the native fish community, and the potential for genetic alteration of wild fish stocks.

TROPHIC EFFECTS

The farming of salmonids in freshwaters generally occurs in oligotrophic systems and, therefore, the addition of byproducts of feed assimilation (primarily P and N), may result in the increased productivity of receiving waters. In extreme cases, eutrophication may result, although this has only been reported in mine pit lakes (Axler et al. 1996). No Canadian study has specifically examined the trophic alteration of freshwater food webs as a direct result of aquaculture practices. However, there is a considerable body of literature concerned with cultural eutrophication of freshwaters and we look to this literature for expected effects on native fish communities. The fertilization of freshwaters can increase primary production and standing stocks of zooplankton, resulting in greater in-lake growth of native and stocked fish species (Vinberg and Lyaknovich 1969; Mills 1985). In fact, the fertilization of inland lakes has formed the basis of a successful rehabilitation program to increase the production of juvenile sockeye salmon (*Oncorhynchus nerka*) in British Columbia freshwaters over the past 25 years (Stockner and MacIsaac 1996). For salmonids, this positive response in growth is thought to be a short-term, immediate response to increased nutrients. Longer-term responses to extreme fertilization (i.e., to eutrophic conditions), suggest an inhibition of natural reproduction and a shift from a typical cool-water salmonid community to a warmwater fish community (Colby et al. 1972; Ryder and Johnson 1972; Penczak et al. 1982; Iversen 1995). In addition, native salmonid species may be less tolerant to eutrophic conditions than farmed species, resulting in a shift in fish community that favors escaped fish (Phillips et al. 1985b). Due to the paucity of research in this area, the extent to which present levels of intensive salmonid cage-culture may affect native fish populations through fertilization-related food web alterations of Canadian freshwaters remains unclear.

A more direct route by which intensive cage-culture can result in trophic changes for native fish species is through the consumption of waste feed and faeces (Johansson et al. 1998). There are no recent direct estimates of the proportion of waste feed for farmed freshwater fish, but 15 years ago the range for farmed salt-water Atlantic salmon (*Salmo salar*) fed dry pellets was 1% to 40% (Thorpe et al. 1990). It is generally thought that the amount of feed that passes uneaten through freshwater fish pens is at the lower end of the salt-water estimate (i.e., 1%–5%), but no published data exist for Canadian aquaculture facilities. The combination of excess feed and faecal wastes that collect below aquaculture cages provides a novel food source to native and escaped fishes. A study of the fish community in an oligotrophic lake in Norway showed that native Arctic char (*Salvelinus alpinus*), which switched to consuming waste food from rainbow trout and Atlantic salmon fish farms, attained a significantly larger size than fish at control sites (Gabrielsen 1999). In Scottish lochs, similar results were observed for escaped rainbow trout, where greater total number and weight of escapees occurred beside farm cages than at distant control sites (Phillips et al. 1985b; Carss 1990). Similar findings occurred in a study of escaped rainbow trout in an oligotrophic Canadian lake, where higher catch of escaped trout occurred near the farm and faster rates of growth were observed for trout with greater proportions of waste feed in their diet (Chaine and Whoriskey 1990). The high mobility of native and escaped fish species observed in these studies (e.g., Phillips et al. 1985b; Gabrielsen 1999), along with stomach content analyses and experiments employing indicator particles in waste feed (Borum et al. 1995; Johansson et al. 1998), showed that organic wastes (feed and faeces) can be widely dispersed throughout the aquatic system. Overall there are few quantitative data on the degree to which native or escaped fish feed on aquaculture-derived wastes in freshwater systems. In a Norwegian study, there was feeding on fish-farm waste by one salmonid species in the lake (Carss 1990), while a Swedish study predicted that 100% of the faeces of farmed rainbow trout were consumed by various species of the fish community (Borum et al. 1995). New models are being developed to account for the P bound in native fish through the consumption of waste feed and faeces and then removed from a system by the direct harvest of native fishes (Borum et al. 1995; Håkanson et al. 1998; Johansson et al. 1998). These studies suggest that the dispersion of the wastes associated with aquaculture may greatly reduce the localized effects of waste build-up under pens. Consequently, the effects of aquaculture may be less localized than previously thought because the distribution of wastes can be spread over large areas by native fish species. In summary, a lack of information on the role that native fish play in the binding and dispersion of phosphorus through consumption of waste feed and faeces is a fundamental research gap that needs to be resolved if we are to successfully predict the effect of aquaculture P inputs on aquatic ecosystems in Canada.

NATIVE – FARMED FISH INTERACTIONS

The development of aquaculture has led to the presence of escaped farmed fish in the wild, often well outside of a species' natural range (Welcomme 1988). It is now recognized that species interactions, especially those from the establishment of self-sustaining introduced species or the alteration of indigenous gene pools, are potentially the most damaging consequences of aquaculture (Arthington and Bluhdorn 1996). This is because effects on indigenous biota are often irreversible while the environmental effects of aquaculture on local habitats can, for the most part, be managed or at least minimized through activities such as appropriate facility-siting (Beveridge and Stewart 1998).

There are no published estimates of the numbers of farmed fish that escape freshwater net pens in Canada. Phillips et al. (1985b) suggest that escaped fish represent approximately 3% to 5% of total cage production. The incidence of escapes is related primarily to the type of culture operation; more infrastructure is available to prevent escapes in intensive fish culture operations than in semi-intensive or extensive ones (Bergan et al. 1991). The practice of cage-culture in freshwaters results in a high probability of farmed fish escaping into surrounding waters and is due to many of the same risks that occur in marine systems – storm damage, ice damage, collision with ships, vandalism, and accidental losses associated with handling (NCC 1990). Many of these events tend to result in the release of a large number of farmed fish into the environment in a short time period. For example, the escape of almost half a million rainbow trout from a cage-culture operation in Lake Diefenbaker, Canada, was due to ice damage (The Leader-Post, Regina, May 16, 2000). The fate of large numbers of farmed fish in oligotrophic lakes and their interactions with native fish are an un-documented concern for the Canadian aquaculture industry and this is a knowledge gap.

EFFECTS ON NATIVE FISH COMMUNITIES

Interactions between native and farmed fish have the potential to result in negative effects on the viability of native populations (Holcík 1991; Youngson and Verspoor 1998). These interactions need not include successful reproduction by farmed fish to affect the native fish community (Arthington and Bluhdorn 1996). The escape of farmed salmonids is not necessarily equivalent to the introduction of the same species for stocking and management purposes in freshwaters because different broodstocks may be used. Many aquaculture species are subject to breeding programs that select for economically important traits such as rapid growth (Bridger and Garber 2002). Also, divergence in behavior between native and domesticated fish increases with the length of time a fish is domesticated (Jonsson 1997). Therefore, interactions between farmed fish escapees and native fish may be very different from those between stocked and native fish. For example, selection for higher growth rates, which causes increased juvenile aggression among farmed salmonids (e.g., Gross 1998), may exacerbate disruptive behavioral interactions between escapees and native fishes.

The ecological and genetic effects of salmonid introductions in North America have been the topic of several reviews (Krueger and May 1991; Crawford 2001). Predation and the competition for limited resources are the principal processes by which introduced fish can alter the native fish community. It is important to recognize that the introduction of an additional species, or greater number of a given species, into an ecosystem will likely result in some redistribution of resources among members of the fish community

(Arthington and Bluhdorn 1996). The characteristics that favor certain species for aquaculture (i.e., generalists with broad environmental tolerances) are those that may also promote the success of these species when introduced into foreign water bodies.

The rainbow trout is perhaps the most widely introduced North American freshwater fish species. Its natural distribution was west of the Rocky Mountains, ranging from Mexico to Alaska, but now encompasses a broader distribution across North America (Scott and Crossman 1973; Crawford 2001); it has also been introduced into 82 other countries (Welcomme 1988). These introductions have repeatedly caused the loss of native salmonid and non-salmonid species (Rosenthal 1980; Welcomme 1988; Crowl et al. 1992; and Cowx 1997). The effects of non-native salmonid introductions can be extreme and introductions to lentic versus lotic systems or to communities that lack a native, top-level piscivore are more likely to result in extirpation of native fish populations (Crowl et al. 1992). To date, most research on the interaction between farmed and native salmonids has focused on competitive experiments using either juvenile or reproductively active adults with very little research at other life-history stages. One area that has received little attention, but is of increasing importance, is the loss of threatened native species through predation by non-native salmonids (Rinne and Alexander 1995).

Although the published literature suggests that the introduction of non-native salmonids has the potential to affect native populations, it should be noted that in Ontario cage culture occurs only in ecosystems into which rainbow trout have already been introduced, typically through provincial stocking programs. Initial stocking of rainbow trout into the Laurentian Great Lakes occurred over a century ago and this species now maintains self-sustaining populations throughout these lakes (Crawford 2001). There are no published studies that specifically describe the interactions of escaped farmed rainbow trout with species originally native to the Great Lakes or with self-sustaining populations of introduced fish species. The magnitude of the effect of escapees when put into context of that of deliberate stocking is not known. The following discussion, therefore, will focus on interactions between rainbow trout (not specifically escapees) and other fish species. In Canadian waters, there is growing evidence that rainbow trout are a potential threat to the reintroduction of native Atlantic salmon into the Great Lakes, either through direct competition at the juvenile stage or predation by large piscivorous adults (Gibson 1981). In streams, space (i.e., feeding territories) is often a limiting resource for which juvenile salmonids compete (Grant and Kramer 1990). A study in Ontario has found that when in competition with rainbow trout, Atlantic salmon juveniles tend to become displaced from their territory, resulting in greatly reduced survival and growth (Jones and Stanfield 1993). Similarly, on the breeding grounds, spawning sites are often limiting. In Canadian waters, there are concerns that the later spawning times of rainbow trout result in them out-competing brown trout (*Salmo trutta*), a non-native fish that now maintains self-sustaining populations. In a New Zealand study, increased egg mortality due to site reuse and the elimination of a brown trout population have been observed when in competition with rainbow trout (Scott and Irvine 2000). Rainbow trout out-compete brown trout and brook trout (*Salvelinus fontinalis*) for food resources and can cause declines in these populations (Kerr and Grant 1999).

The majority of freshwater cage aquaculture in Canada occurs in the North Channel of Lake Huron and the interaction of escaped or stocked rainbow trout and lake trout (*Salvelinus namaycush*) may be of concern to local stakeholders. Fraser (1972) reported poor recovery of introduced hatchery-reared rainbow trout in selected Ontario lakes, particularly when the native fish community contained lake trout and brook trout. There has been a steady increase observed in catch per unit effort of wild lake trout in Canadian waters of the Great Lakes since the mid-1970s (Bronte et al. 2003) despite stocking programs adding millions of rainbow trout to these lakes (Crawford 2001). Recent dietary studies of lake trout and naturalized rainbow trout in Lake Superior (Conner et al. 1993) and Lake Michigan (Jude et al. 1987) showed little overlap, and Kitchell et al. (2000) and Bronte et al. (2003) also report minimal dietary overlap and differences in thermal tolerances and life-history characteristics. However, unpublished results from an investigation of the escape of 36,000 rainbow trout fingerlings from a cage in an oligotrophic lake in Quebec suggest that there is potential for competition with lake trout in diet and pelagic distribution (Chaine and Whoriskey 1990). Little is known of the feeding ecology or pelagic distribution of escaped fish and further research is important to determine if concerns over interactions with lake trout are warranted.

There is relatively little information on the behavior and long-term success of escaped fish. Whole-lake experimental comparisons of farmed and wild rainbow trout provide clear evidence that farmed fish are maladapted to survive in the presence of predators (Biro et al. 2004). Two studies have used telemetry to monitor the movements of a farmed rainbow trout after planned "escapes" from cage facilities. One study in a Scottish loch examined one fish for about a 3-day period and showed that this fish remained close to cage-culture operations but also made extensive forays throughout the small loch (Phillips et al. 1985b). Escaped rainbow trout in a coastal Newfoundland study showed fidelity to cage sites, but also moved among the various cage sites within the area (Bridger et al. 2001). These studies point to a dependence of escaped rainbow trout upon the cage sites for food, but their high mobility and wide dispersion also allows for interactions with native fish species. The degree to which farmed salmonids and native or naturalized species interact and the outcome of these interactions is an area that warrants further research in Canadian ecosystems so as to increase public confidence in the sustainability of this industry.

GENETIC INTERACTIONS

The extent of any permanent effect of escaped species relies on its successful reproduction in the wild, be it with other farmed, stocked or native fish of the same species (e.g., (Youngson and Verspoor 1998), or through hybridization with closely related species (e.g., (Hindar and Balstad 1994). There has been extensive research into the reproductive success of salmonid escapees and genetic interactions with their wild counterparts, including several recent reviews (e.g. Jonsson 1997). In summary, farmed fish that escape cage-culture facilities are able to grow, mature, and reproduce with native fish in the wild. Overall, the reproductive success of farmed fish is much lower than that of native fish (e.g., ~16% of that for native fish; Fleming et al. 2000). The traits selected in aquaculture breeding programs can differ significantly from those necessary for survival in the wild. Interbreeding of farmed and native fish could produce long-term genetic changes that are detrimental in natural populations (Gross 1998). Recent studies of escaped Atlantic salmon on wild populations provide clear evidence that escaped fish can reduce the genetic diversity of native salmon populations and result in much lowered fitness of "hybrid" (wild x farm) fish (McGinnity, et al. 1997; Einum and Fleming 1997; McGinnity et al. 2003).

There are no Canadian studies on the genetic interaction of escaped farmed fish and their wild counterparts, or hybridization of farmed and wild fish. In the U.K., evidence for self-sustaining populations of rainbow trout occur in only 1% of waters where escapees are present, suggesting that this species has been generally unable to breed successfully (Frost 1974). Rainbow trout were deliberately stocked in Lake Huron starting in 1876 (Emery 1985) and slightly later in the other Great Lakes (Lawrie and Rahrer 1972; Christie et al. 1972). Annual stocking of rainbow trout has continued since the mid-1960s (Emery 1985; MacCallum and Selgeby 1987; Crawford 2001). Farmed rainbow trout from various hatcheries show genetic divergence in traits such as growth (Ferguson and Danzmann 1999), and may differ from naturalized populations. Studies comparing the relative reproductive success of hatchery-reared and naturalized steelhead trout from the Pacific west coast (Washington, USA) showed that naturally spawning hatchery steelhead had lower reproductive success than did wild fish. However, a large contribution of smolts produced by hatchery fish occurred because of their numerical advantage over wild spawning fish (Chilcote et al. 1986; Leider et al. 1990). Given that rainbow trout are currently stocked annually into the Laurentian Great Lakes, is difficult to determine the precise effect escaped farmed fish versus stocked hatchery fish will have on locally adapted naturalized populations.

In summary, there is a large body of literature that addresses the genetic effects of introduced species on native populations. However, there is very little specific information about the genetic interactions of farmed and native fish in Canadian freshwaters. Numerous studies show hybridization between native and introduced populations of rainbow trout (e.g., Campton and Johnston 1985; Carmichael et al. 1993; Williams et al. 1996), including threatened species of trout (Dowling and Childs 1992). In Canadian freshwaters, the opportunity for hybridization between farmed and naturalized or native fish of the same species will depend on the species being cultured and those present in the system. Rainbow trout accounts for the majority of freshwater aquaculture in Canada and its potential to hybridize with naturalized populations is likely limited (Kerr and Grant 1999). Recent development of risk-assessment protocols for cage-culture in the Great Lakes (Brister 2003) provides a starting framework to minimize genetic interactions between native and farmed fish.

KNOWLEDGE GAPS AND RESEARCH NEEDS

In general, there is a considerable lag between the state of research on the environmental effects of aquaculture on freshwater ecosystems and that in the marine environment, which are fairly well documented. Our scientific knowledge of effects of freshwater aquaculture comes primarily from a limited number of European studies. The University of Guelph has produced a considerable and valuable body of research on waste loading under varying husbandry practices. Using methods developed by Dr. C.Y Cho and Dr. D.P. Bureau at the University of Guelph, it is now feasible to predict waste loading from an aquaculture facility based on the feed composition, water temperature, and fish number and size (Cho and Bureau 1998). Scientific knowledge of the effects of this waste loading on Canadian freshwater ecosystems is, however, almost completely lacking. At the time of writing, merely three studies exist (Cornel and Whoriskey 1993; MacIsaac and Stockner 1995; Hamblin and Gale), only two of which are published in the primary literature. The first two are likely outdated due to advances in the aquaculture industry. What follows is a list of areas that require further research to adequately understand the effects of aquaculture on freshwater aquatic environments, and thereby contribute to the sustainability of this industry.

- No scientific information is available in the literature on the current waste feed levels or feed conversion ratios at commercial freshwater finfish facilities in Canada. Although there are many FCR reported in the literature, for the most part they were generated under experimental rather than commercial operating conditions. Furthermore, future research projects should report the FCR, annual production rate, and nutrient content of feed used at study sites.

- There is a lack of published scientific information on the effects of freshwater aquaculture activities on benthic habitats. This is the component of habitat most likely affected by aquaculture waste. Research is needed to quantify the extent of accumulations under commercial finfish farms and to understand the factors – both hydrologic and biotic – that may affect the rate of accumulation. Additionally, the relationship between accumulation of wastes and changes in sediment characteristics and in benthic invertebrate communities is needed. It is likely that at a moderate level of waste accumulation, the primary effects are enrichment and adverse effects are seen only above a threshold. Where this threshold is and how these effects develop is an area requiring further research.

- Research is needed to develop an understanding of how phosphorus, nitrogen, and carbon from aquaculture facilities cycle in the freshwater environment. In particular, research is needed to understand the fate of aquaculture inputs of phosphorus and the relationship between aquaculture nutrient loading and the resulting effects on water quality and primary productivity.

- There are very limited scientific data on the effects of aquaculture wastes on the species composition and productivity of freshwater primary producers, zooplankton, or on microbial communities. Also, no scientific information is available on the extent to which present levels of intensive salmonid cage-culture affect native fish populations through trophic alterations of Canadian freshwater ecosystems.

- Research is needed on the role that native (and escaped) freshwater fish play in the binding and dispersion of phosphorus through consumption of waste feed and faeces if we are to successfully develop predictive models on the amount of P input into aquatic ecosystems and the sustainability of freshwater aquaculture.

- There is also a need for accurate estimates of the number of escaped fish entering freshwater systems, and a determination of their role in aquatic ecosystems at all life-history stages.

- There are very few studies documenting the interactions between native and farmed fish in freshwaters. The degree to which native and farmed salmonids interact and the outcome of these interactions is an area that warrants further research in freshwaters.

- There is very little specific information about the genetic interactions of farmed and native fish in Canadian freshwater lakes where most of the aquaculture industry is currently based.

- An assessment of the degree to which sterile, triploid fish are farmed in Canadian freshwaters and the efficacy of treatments to induce triploidy are needed to assess the risks of current aquaculture practices in affecting native gene pools.

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A SCIENTIFIC REVIEW OF BIVALVE AQUACULTURE: INTERACTION BETWEEN WILD AND CULTURED SPECIES

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EXECUTIVE SUMMARY

This paper reviews the present state of knowledge on interactions between wild and cultured species within the context of bivalve mariculture in Canada. It also identifies critical knowledge gaps and recommends research to address these gaps. The literature reviewed includes national and international information covering bivalve aquaculture, bivalve restoration, coastal community and ecology. This review is focused on changes affecting the pelagic community, benthic communities, predator species, genetic structures, and the risk of introducing invasive species.

PELAGIC COMMUNITY AND BIVALVE CULTURE INTERACTIONS

Bivalve aquaculture has two main effects on the pelagic community. First, as grazers, bivalves reduce the phytoplankton biomass that may affect the productivity of other grazing species. Limited information is available on this potential effect of bivalve aquaculture, and to date this has only been demonstrated through the use of ecosystem models. The second main effect of bivalve aquaculture on the pelagic community is via the creation of additional habitat in the water column. This is supported mainly by studies on the effect of shellfish restoration, which clearly show that three-dimensional oyster reefs increase the biomass and possibly productivity of several pelagic species benefiting from food availability or predator avoidance. Although these extrapolations may be logical, direct evidence of these interactions is lacking. Research is recommended to address the:

- *effect of bivalve aquaculture on phytoplankton production and the grazing community.*
- *effect of the epifaunal community associated with bivalve aquaculture on the nekton community.*

BENTHIC COMMUNITY AND BIVALVE AQUACULTURE INTERACTIONS

Macrobenthic communities affect rates, directions, and pathways of the exchange of energy and materials between the water column and the sediment, and are critical in regenerating nutrients via benthic-pelagic coupling mechanisms. Shifts in benthic community structure and functioning due to biodeposition, physical alterations, and the presence of fouling organisms have been noted in the proximity of bivalve aquaculture operations, however, the extent of these changes are variable. Preliminary data suggest that bivalve aquaculture may increase coastal productivity. Research recommendations are as follows:

- *examinations of the influence of bivalve aquaculture on second order relationships such as growth or reproduction of ecologically and/or commercially important species are required;*
- *knowledge of interactions related to seagrass communities is incomplete; hypotheses addressing growth rates and distributions of seagrass at near-field and far-field scales need to be tested to provide information for resource managers to effectively protect these areas without unnecessarily hindering the development of this burgeoning industry;*
- *the spatial scale of resolution on which research questions are based needs to be expanded from the lease-scale to address hypotheses of estuary/bay-wide ecological changes to structure, function, and productivity of benthic communities; and*
- *the potential for cumulative effects (municipal wastewater processing, fish processing plants, agricultural inputs, pulp and paper effluents, etc.) in conjunction with bivalve aquaculture on benthic ecosystem change needs to be assessed.*

PREDATOR EFFECTS RELATED TO BIVALVE CULTURE

Research conducted on the relation between predators and bivalve aquaculture is primarily focused on the effect of predators on cultured bivalves. These studies deal mainly with predator control and exclusion methods. These methods have only been investigated on a local scale; their effects from an ecosystem perspective have not yet been addressed. The effect of aquaculture activities on predator densities is not clearly defined; some studies suggest aggregation of predators while others do not. In studies with increased predator densities, it is unclear if this is due to the aggregation of existing populations or an increase of the population. Research gaps that need to be addressed are as follows:

- *effect of predator management methods on targeted and non-targeted species.*
- *effect of bivalve aquaculture on the abundance and distribution of predators.*

EXOTIC SPECIES RELATED TO BIVALVE AQUACULTURE

Historically, the introduction and transfer of bivalves for aquaculture has been one of the most important vectors for the introduction of exotic species around the world. This includes the bivalves that have been intentionally introduced into an area for aquaculture purposes – the "target" species, the animals and plants (both macroalgae and phytoplankton) that grow associated with the introduced bivalves – "hitchhiking" species, and diseases. Introduced bivalves are engineering species and may thus have a large influence on many aspects of the ecology of the receiving area. These changes may further facilitate the introduction and growth of other exotic species. Both target and hitchhiking species may have a variety of cascading effects on the receiving ecosystem. However, research on the subject is extremely limited and many such effects are simply theoretical. Ideally, thorough risk assessments should be done before any introductions and transfers are authorized. Quarantine, disinfection, and other protocols may be used to limit risk. However, the efficacy of such treatments is not always great and other measures should be considered. A number of research needs were identified to better understand and minimize the potential role of bivalve aquaculture in increasing the rate of introduction, spread and effect of exotic species. These include the following:

- *preliminary risk analyses, as outlined in the section on management issues, should be done to identify knowledge gaps with respect to exotic species in bivalve culture (the cultured bivalves themselves and hitchhiking species);*
- *directed research should be used to address these knowledge gaps prior to the introduction of bivalves into a system for aquaculture;*
- *obtain baseline information on the receiving environment (physical and biological) to make predictions with respect to exotics and to evaluate and understand their influence;*
- *predict the ability of exotics to establish and spread in the receiving environment; and*
- *predict the effects of exotic species on receiving ecosystems, including interactions with local species, habitat modifications, energy flow, etc.*

More information is needed on the requirements and influence of hitchhiking species in the environment. This is particularly true for a number of currently problematic species (e.g., tunicates). Specifically,

- *more information is needed with respect to the natural history of most exotic species;*
- *more information is needed with respect to the relative importance of natural (currents, dispersion rates, etc.) and anthropogenic (stock transfers, processing, hull fouling, etc.) spread of exotic species;*
- *remedial measures need be developed to mitigate effects and minimize spread; and*
- *research is needed to understand the links between the presence of exotic species and other stressors in the environment (e.g., eutrophication, climate change, fishing activities, contamination, etc.).*

EXAMEN SCIENTIFIQUE DE L'ÉLEVAGE DE BIVALVES : INTERACTION ENTRE LES ESPÈCES D'ÉLEVAGE ET LES ESPÈCES SAUVAGES

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SOMMAIRE

Cet article porte sur l'examen de l'état actuel des connaissances sur les interactions entre les espèces d'élevage et les espèces sauvages dans le contexte de l'élevage de bivalves en milieu marin au Canada. De plus, nous y cernons les lacunes dans les connaissances qui ont une importance particulière et nous recommandons des projets de recherche pour combler ces lacunes. Nous avons passé en revue les ouvrages canadiens et étrangers contenant de l'information sur l'élevage, le rétablissement, les communautés côtières et l'écologie des bivalves. Le présent examen est axé sur les changements qui ont une incidence sur la communauté pélagique, les communautés benthiques, les prédateurs, les structures génétiques et le risque d'introduction d'espèces envahissantes.

INTERACTIONS ENTRE LES BIVALVES D'ÉLEVAGE ET LA COMMUNATUÉ PÉLAGIQUE

L'élevage de bivalves a deux effets principaux sur la communauté pélagique. D'abord, à titre de brouteurs, les bivalves réduisent la biomasse de phytoplancton, ce qui peut avoir une incidence sur la productivité d'autres espèces de brouteurs. Peu de données sont disponibles sur cet effet possible de l'élevage de bivalves, et, à ce jour, seuls des modèles écosystémiques ont mis cet effet en évidence. Le deuxième effet principal de l'élevage de bivalves sur la communauté pélagique est une conséquence de la création d'habitats supplémentaires dans la colonne d'eau. Cet effet a été mis en évidence principalement par des études sur les conséquences du rétablissement de mollusques, qui montrent clairement que les bancs d'huîtres en trois dimensions entraînent une augmentation de la biomasse et du potentiel de productivité de plusieurs espèces pélagiques, celles-ci profitant de la disponibilité de ressources alimentaires ou des possibilités d'évitement des prédateurs. Même si ces extrapolations peuvent être logiques, il n'y a toujours pas de preuve directe de telles interactions. Nous recommandons que des recherches soient menées sur les sujets suivants :

- *les effets de l'élevage de bivalves sur la production de phytoplancton et sur la communauté de brouteurs;*
- *les effets de la communauté épifaunique associée à l'élevage de bivalves sur le necton.*

INTERACTIONS ENTRE LES BIVALVES D'ÉLEVAGE ET LA COMMUNAUTÉ BENTHIQUE

Les communautés macrobenthiques ont une incidence sur les taux et les voies d'échange d'énergie et de matières entre la colonne d'eau et les sédiments, de même que sur les orientations de ce type d'échange, et elles sont essentielles à la régénération des éléments nutritifs par l'intermédiaire de mécanismes de liaison entre le milieu benthique et le milieu pélagique. Des changements sur le plan de la structure et du fonctionnement de la communauté benthique, dus aux biodépôts, à des modifications du milieu physique et à la présence de salissures marines, ont été signalés à proximité de sites d'élevage de bivalves. L'ampleur de ces changements est toutefois variable. Les données préliminaires suggèrent que l'élevage de bivalves pourrait accroître la productivité en milieu côtier. Nos recommandations de recherche sont les suivantes :

- *l'examen de l'incidence de l'élevage de bivalves sur les relations de deuxième ordre, telles la croissance ou la reproduction d'espèces importantes sur le plan écologique ou commercial;*
- *l'approfondissement des connaissances sur les interactions liées aux communautés de graminées marines; la vérification d'hypothèses relatives aux taux de croissance et à la répartition des graminées marines à petite et à grande échelle afin de fournir de l'information aux gestionnaires des ressources dans le but de protéger efficacement ces communautés sans nuire inutilement au développement de l'industrie florissante de l'élevage de bivalves;*
- *l'amélioration de l'échelle spatiale sur laquelle les recherches sont fondées, à partir de l'échelle des concessions, afin de vérifier les hypothèses relatives aux changements écologiques sur le plan de la structure, de la fonction et de la productivité des communautés benthiques à l'échelle des baies et des estuaires;*
- *l'évaluation de la probabilité d'effets cumulatifs (traitement des eaux usées municipales, usines de transformation du poisson, intrants agricoles, effluents d'usines de pâtes et papiers, etc.), en liaison avec l'élevage de bivalves, sur l'écosystème benthique.*

EFFETS DES PRÉDATEURS LIÉS À L'ÉLEVAGE DE BIVALVES

La recherche portant sur la relation entre les prédateurs et l'élevage de bivalves est centrée principalement sur les effets des prédateurs sur les bivalves d'élevage. Ces études sont axées sur la gestion des prédateurs et les méthodes d'exclusion. Ces méthodes ont fait l'objet d'études à l'échelle locale seulement, et leurs effets à l'échelle des écosystèmes n'ont pas encore été examinés. Les effets des activités aquacoles sur la *densité des prédateurs ne sont pas établis clairement, certaines études suggérant un regroupement des prédateurs et d'autres indiquant l'inverse. Dans le cas des études qui suggèrent une hausse de la densité des prédateurs, il n'est pas établi clairement si cette hausse est due à un regroupement de populations existantes ou à une hausse de l'effectif de la population. Les lacunes qui doivent être comblées sont les suivantes :*

- *les effets de méthodes de lutte contre les prédateurs sur les espèces ciblées et non ciblées;*
- *les effets de l'élevage de bivalves sur l'abondance et la répartition des prédateurs.*

ESPÈCES EXOTIQUES LIÉES À L'ÉLEVAGE DE BIVALVES

Historiquement, l'introduction et le transfert de bivalves aux fins d'aquaculture a été l'un des vecteurs d'introduction d'espèces exotiques les plus importants partout dans le monde. Ces espèces exotiques comprennent les bivalves qui ont été introduits de manière intentionnelle dans une zone aux fins d'aquaculture, c.-à-d. les espèces cibles ainsi que les animaux et les plantes (à la fois les macroalgues et le phytoplancton) qui sont associés aux bivalves introduits, les auto-stoppeurs et les maladies. Les bivalves introduits sont des espèces qui peuvent avoir une grande incidence sur de nombreux aspects de l'écologie du milieu récepteur. Ces changements peuvent faciliter davantage l'introduction et la croissance d'autres espèces exotiques. Les espèces cibles et les auto-stoppeurs peuvent entraîner une cascade d'effets divers sur l'écosystème récepteur. Cependant, la recherche sur le sujet est très limitée, et nombre de ces effets sont uniquement théoriques. Idéalement, des évaluations approfondies des risques devraient être effectuées avant l'autorisation de toute introduction ou de tout transfert. La quarantaine, la désinfection et d'autres protocoles peuvent être utilisés pour réduire les risques. Cependant, l'efficacité de tels traitements n'est pas toujours élevée et d'autres mesures devraient être envisagées. Un certain nombre de besoins de recherche ont été cernés afin de mieux comprendre et de réduire au minimum le rôle possible de l'élevage de bivalves dans la hausse du taux d'introduction, de la propagation et des répercussions des espèces exotiques. Parmi les besoins de recherche, il convient de mentionner les suivants :

- *la réalisation d'analyses des risques préliminaires (voir la section sur les questions de gestion) afin de cerner les lacunes dans les connaissances sur les espèces exotiques liées à l'élevage de bivalves (les bivalves d'élevage eux-mêmes et les auto-stoppeurs);*
- *la réalisation de travaux de recherche ciblés pour combler ces lacunes dans les connaissances avant l'introduction de bivalves dans un système aux fins d'aquaculture;*
- *l'obtention de données de référence sur le milieu récepteur (physiques et biologiques) afin d'établir des prévisions relatives aux espèces exotiques ainsi que d'évaluer et de comprendre les effets de celles-ci;*

- *la prévision de l'habilité des espèces exotiques à s'établir et à se propager dans le milieu récepteur;*
- *la prévision des effets des espèces exotiques sur les écosystèmes récepteurs, y compris leurs interactions avec les espèces indigènes, les modifications sur le plan de l'habitat, les transferts d'énergie, etc.*

Il est nécessaire d'obtenir plus de renseignements sur les besoins et l'incidence des auto-stoppeurs dans l'environnement, particulièrement dans le cas d'un certain nombre d'espèces qui posent des problèmes (p. ex. tuniciers). Il convient notamment de satisfaire les besoins suivants :

- *obtenir plus de données sur l'histoire naturelle de la plupart des espèces exotiques;*
- *obtenir plus de données sur l'importance relative de facteurs naturels (courants, taux de dispersion, etc.) et anthropiques (transferts de stocks, transformation, salissures sur la coque de navires, etc.) liés à la propagation des espèces exotiques;*
- *élaborer des mesures correctives afin d'atténuer les effets et de réduire au minimum la propagation;*
- *approfondir les connaissances sur les liens entre la présence d'espèces exotiques et d'autres facteurs stressants dans l'environnement (p. ex. eutrophisation, changement climatique, activités de pêche, contamination, etc.).*

INTRODUCTION

Aquaculture is a relatively new sector of the Canadian agri-food industry. Currently, the culture of salmonid species in the Atlantic and Pacific regions accounts for more than three-quarters of Canadian production while the remainder is dominated by bivalve culture of oysters in British Columbia and the Maritime provinces and mussels in Prince Edward Island.

Canada's aquaculture industry has witnessed impressive production increases over the past two decades. Its growth has been dominated by a 33-fold increase in salmonid production since 1986 (Canadian Aquaculture Production Statistics, DFO 2005). This high rate of growth combined with limited public knowledge of this industry has raised questions about related environmental effects. As such, numerous and extensive studies on this topic have been conducted with stringent regulatory and management plans resulting (reviewed by Hargrave et al. 2003; Wildish et al. 2004).

The bivalve culture industry in Canada has also seen increased growth. Blue mussel (*Mytilus edulis*) production has increased 11-fold over the past two decades and constitutes over 60% of current Canadian bivalve aquaculture production valued at over $32 million/year (Canadian Aquaculture Production Statistics 2004). Oyster aquaculture has also seen similar growth trends (4-fold increase nationally) and in New Brunswick alone, recent market projections have further estimated a 5-fold increase in suspended oyster production by 2010 (Unic Marketing Group Ltd. 2003).

To date, there have been fewer studies on the potential interactions between bivalve culture and the marine environment compared to finfish aquaculture. However, due to these recent and projected production increases combined with findings of negative environmental interactions attributable to finfish aquaculture activities (Hargrave et al. 2003; Wildish et al. 2004), serious questions are being raised in regard to the potential for negative interactions between cultured bivalves and coastal ecosystems. As a further complication, there is also a growing body of literature supporting potentially positive environmental aspects of bivalve aquaculture (reviewed by Newell 2004). To develop effective management strategies for coastal zones that permit sustainable development of this expanding industry, it is crucial to have accurate, current information on the direction, magnitude, and timing of spatial and temporal interactions with surrounding (supporting) ecosystems. This is especially critical in light of diminishing production from traditional harvest fisheries in the coastal zone, declining environmental quality from nutrient and other pollution, and increasing pressure to expand employment opportunities for rural coastal communities.

The intention of this review is to complement previous contributions to the Statement of Knowledge (SOK) series on environmental interactions of aquaculture activities. Previously, Hargrave et al. (2003) examined the effects of wastes, chemicals used by the industry, and far-field interactions between farmed finfish/bivalves and wild species (including disease transfer, and genetic and ecological interactions). With recent advances in our understanding of environmental interactions related to bivalve aquaculture, our goal is to provide an update to Hargrave et al. (2003) with the most current scientific information that deals solely with bivalve aquaculture. Specifically, the current review summarizes information available from the scientific literature on environmental interactions (both positive and negative) between cultured bivalves and coastal ecosystems with detailed emphasis on ecological effects pertaining to the cultured organisms, their required infrastructure, and industry practices (set-up, harvesting, and maintenance), both on near- and far-field scales. Knowledge gaps are identified and areas of research to address these gaps are recommended. This review is divided into five sections: Pelagic Community Interactions, Benthic Community Interactions, Predator Effects, Genetic Interactions, and Invasive Species Interactions.

PELAGIC COMMUNITY AND BIVALVE CULTURE INTERACTIONS

Biodiversity is often used to measure anthropogenic effects on community health; however, few studies were found evaluating the effects of shellfish or finfish aquaculture on the biodiversity of pelagic fauna. Of those studies, most focused on finfish aquaculture (Dempster et al. 2002, 2004, Machias et al. 2004). All of these studies found increased numbers and biomass of pelagic fish around fish cages. Most aquaculture and biodiversity studies focus on benthic (Kaiser et al. 1998) or phytoplankton communities (Ball et al. 1997, Newell 2004). Ball et al. (1997) investigated the assumption that intense bivalve culture would deplete phytoplankton biomass, which, in turn, would affect pelagic biodiversity (especially the grazing zooplankton community) as a result of competition for limited food resources.

Models are used increasingly to estimate the carrying capacity of an ecosystem. ECOPATH, a model based on food webs, was used in New Zealand to estimate the production carrying capacity of green mussel aquaculture (Gibbs 2004; Jiang and Gibbs 2005). The biomass of all trophic levels is introduced in the model. By modifying some of the parameters – namely the biomass of bivalves – the authors were able to predict the potential effects of the introduction of aquaculture. Some species of pelagic fish experienced a positive effect while others a negative effect. Bivalves feed on phytoplankton and small zooplankton therefore they will affect these groups directly (Jiang and Gibbs 2005). They will also have an effect on large zooplankton as competitors. These effects will cascade to the higher trophic levels (Jiang and Gibbs 2005) according to their dependence on phytoplankton and zooplankton. Models such as ECOPATH can be useful in estimating what level of production of bivalves cause acceptable changes in the ecosystem.

The infrastructure used in bivalve culture can frequently act as an artificial reef as well as fish aggregation devices (Costa-Pierce and Bridger 2002; Nelson 2003). They increase the productivity of a system over the short and long term. Mussel seed ropes are good examples of the short-term increase in productivity and biodiversity. Gonzalez Sanjurgo (1982) showed that although mussel seed accounted for 95% of the total biomass collected on ropes, the remaining 5% comprised more than 70 invertebrate species. Similar results have been reported on mussel socks over a longer time period (Ellis et al.

2002; LeBlanc et al. 2003; Lopez-Jamar et al. 1984) and for oyster tables and scallop lines (Lamy et al. 1998; Perera et al. 1990; Soldatova et al. 1985). The increased productivity and biodiversity stemming from the epifauna on the culture infrastructure also effects the nekton populations that prey on them (mussel culture – Lopez-Jamar et al. 1984; Fernandez et al. 1995; Freire and González-Gurriarán 1995; oyster reefs – Breitburg 1999; Coen et al. 1999; Harding and Mann 1999; Posey et al. 1999; Luckenbach et al. 2000). Pelagic fish also feed on epifauna. Many species of pelagic fish use aquaculture facilities as nursery areas, as feeding grounds or for protection (Costa-Pierce 2002; Nelson 2003).

Population enhancement is commonly viewed as an aquaculture activity and therefore results from studies on oyster reef restoration can also provide information on the effects of bivalve aquaculture on biodiversity in specific coastal areas. Three-dimensional structures such as oyster reefs are highly heterogeneous and can encourage complex trophic networks by providing refuges, nurseries, and feeding grounds for fish (Harding and Mann 2000). Fish found on reefs are classified in three categories: resident, semi-resident, and transient (Harding and Mann 1999, 2000; Breitburg 1999; Luckenbach et al. 2000; Posey et al. 1999; Coen et al. 1999). Resident species such as the naked gobies and striped blennies use oyster reefs for feeding, shelter and nesting habitat (Breitburg 1999; Harding and Mann 1999, 2000). They use unfouled, articulated oyster shells to shelter their eggs and the larvae selectively feed on bivalve veligers (Harding and Mann 1999). The larvae are, in turn, prey for juvenile striped bass (Breitburg 1999; Harding and Mann 1999, 2000). Posey et al. (1999) found similar results in South Carolina where shrimp used the oyster reefs for refuge, which stimulated increased foraging by mummichogs. The larvae of oysters, gobies and blennies residing on the reefs further contribute to the diet of plankton eating fish (Coen et al. 1999). Harding and Mann (1999) found 32 species of fish representing 26 families on or near Palace Bar Reef (Piankatank River, Virginia, USA). Breitburg (1999) found 17 fish species from 14 families at Flag Pond near the Patuxent River, Maryland, but neither study compared reef sites with non-reef sites.

Studies on artificial reefs would contribute to our knowledge of the effect of bivalve culture infrastructure on productivity and biodiversity. In a review of studies on Mediterranean artificial reefs, Ardizzone et al. (1996) found that the number and composition of reefs depended on sampling methods, geographic location and sediment type. Reefs located on soft bottoms were commonly colonized by species newly recorded for those areas, while reefs located on rocky bottoms were colonized by species found in the vicinity. Some authors argue that artificial reefs simply concentrate biomass rather than increase production (Grossman et al. 1997; Relini and Relini 1996). Yet, a few studies are showing that the higher reproductive output of fish associated with artificial reefs is an indicator of the increased productivity of these systems (Relini and Relini 1996).

KNOWLEDGE GAPS AND RECOMMENDED RESEARCH

The main gaps in knowledge of pelagic interactions with bivalve culture related to the changes in biodiversity and productivity of: 1) the grazing community, 2) the infrastructure epifauna, and 3) the nekton community.

Food competition between cultured species and the indigenous grazing fauna, particularly zooplankton, will be influenced by the composition of the grazing community. Further studies are needed on the temporal and spatial distribution of competing pelagic herbivores in terms of composition and abundance. Information on the overall productivity of the flora and fauna in the water column, relative to the presence and absence of bivalve farming is also required. Information is needed on how changes in epifauna biodiversity resulting from the addition of the culture infrastructure affect the net productivity of an ecosystem and on the interaction between cultured bivalves and epifauna. Further research is needed on the interaction between suspended bivalve culture and the nekton community and should investigate the similarities between aquaculture and artificial reef systems. The two systems may provide similar benefits in respect of increasing productivity and improving reproduction and the recruiting success of fish species. More information is needed on the feeding behaviour of these fish species and the effects that husbandry practices, including harvest activities, have on them.

Replicated treatment sites and the use of adequate reference sites is of great importance to the value of the information generated from these investigations. This is often the weakest point of published studies relating to the interaction between aquaculture and the environment.

BENTHIC COMMUNITY AND BIVALVE AQUACULTURE INTERACTIONS

In aquatic ecosystems, macrobenthic communities affect rates, directions, and pathways of the exchange of energy and materials between the water column and the sediment and are critical in regenerating nutrients via benthic-pelagic coupling mechanisms. Further, these assemblages are vital in mediating the trophic functioning of estuarine systems and their disruption has great potential to alter coastal nutrient processing dynamics (Rakocinski and Zapfe 2005). As such, environmental interactions between aquaculture systems and benthic communities have been studied intensively (Raj 1997). With respect to bivalve aquaculture, these interactions are related to: increased sedimentation and biodeposition due to bivalve feeding/excretion and disruption of local hydrodynamics by culture infrastructure; physical disruption of natural habitat through harvesting practices and substrate enhancement; and, increasing surface area for epibiont attachment and attraction of predators. Each of these interactions, alone or combined, has caused measurable changes to benthic faunal and floral communities through a variety of mechanisms, which will be discussed further. While alteration of nutrient cycling and pathways also influence benthic faunal and floral community dynamics and has been demonstrated in areas of bivalve aquaculture (Kaspar et al. 1985; Kautsky and Evans

1987; Baudinet et al. 1990; Tuttle and Jonas 1992; Barranguet et al. 1994; De Casabianca et al. 1997; Deslous-Paoli et al. 1998; Stenton-Dozey et al. 2001; Mazouni 2004), this topic has recently been reviewed extensively elsewhere (Cranford et al. 2003; Newell 2004) and will not be addressed in this paper.

BIODEPOSITION AND SEDIMENTATION

Filter-feeding bivalves efficiently remove suspended microscopic particulate matter from the water column (Dame 1996) ranging in size from 1 to 7 µm in diameter, depending on species (Cranford et al. 2003). While algae are most often the preferred nutritional source, bivalves may also assimilate detritus, bacteria, and nanozooplankton (Langdon and Newell 1990). Particles that are too large or deemed nutritionally unsatisfactory are subsequently packaged as much larger pellets of pseudofeces and released along with feces (Dame 1996). At times up to 90% of filtered particulate matter may consist of undigested pseudofeces particles with high organic matter content (Hawkins and Bayne 1992). Under natural conditions this process plays a complex role in ecosystem functioning, coupling benthic and pelagic processes through the removal of both phytoplankton and inorganic particles from the water column and influencing nutrient dynamics (Kautsky and Evans 1987; Prins et al. 1998; Newell 2004).

In areas exposed to bivalve aquaculture, this benthic-pelagic coupling is heightened and distinct changes to sedimentation rates (both organic and inorganic) have been observed (Pillay 2004). This situation appears to be caused by increased biodeposition from bivalve feeding combined with reduced current velocities due to culture infrastructure. There is a great potential for current velocity reductions to strongly influence nearshore marine communities on multiple scales. Modifications to local hydrodynamics exert considerable influence on external fertilization, planktonic larval recruitment, nutrient delivery to primary producers, and particulate material flux to suspension- and deposit-feeding organisms (Denny and Wethey 2001). Considerable attention has been given to the influence of flow on macrobenthic faunal communities and Wildish and Kristmanson (1997) have provided an excellent review. Direct observation and modeling studies associated with suspended mussel culture have shown up to 6-fold reductions in current velocities (Boyd and Heasman 1998; Grant and Bacher 2001; Plew et al. 2005). Measurements taken downstream of near-bottom oyster (*Crassostrea gigas*) trestles have noted order of magnitude reductions in current velocity relative to upstream readings (Nugues et al. 1996). Discussion of conflicting conclusions from studies of faunal assemblages surrounding bivalve aquaculture sites with varying hydrodynamic properties is presented later in this review.

Increases in sedimentation rates have also been documented. Dahlbäck and Gunnarsson (1981) estimated that the sedimentation rate under a suspended longline mussel (*Mytilus edulis*) culture site in a Swedish fjord was almost four times that of control areas and that sediment deposition could be up to 1000 g organic carbon $m^{-2}y^{-1}$. Further, Grenz et al. (1990) reported average biodeposits of up to 345 $kg\,m^{-2}y^{-1}$ at a suspended longline mussel (unknown species) culture site in France, but stated this result may have been confounded by deposition from phytoplankton blooms. At off-bottom oyster (*Crassostrea* *gigas*) leases, sedimentation rates of 7000 and 500 g $m^{-2} y^{-1}$ were reported from a foreshore and a pond site, respectively (Martin et al. 1991). In an area of suspended longline mussel (*M. edulis*) aquaculture in Nova Scotia, Cranford and Hill (1999) noted a 26-fold sedimentation rate increase relative to natural conditions. Organic matter content of these deposits was found to range between 20% and 70%. This benthic organic loading may also be supplemented by "fall-off" of large numbers of cultured individuals through mortality and competition for space with epibionts on culture structures (Mattsson and Lindén 1983; Chivilev and Ivanov 1997). Mattsson and Lindén (1983) reported a 7-fold increase in mussel (*M. edulis*) density below a suspended longline lease in a Swedish fjord that had been in operation only one year. Also, the sediment layer of feces and fallen mussels found underneath the lease measured several centimeters. While it is highly likely bivalve feeding is the dominant contributor to these sedimentation increases, more study is needed to better determine the role of current velocity reductions so that its influence can be better mitigated by improved industry management.

ASSEMBLAGE CHANGE

Fluxes of organic matter to benthic environments may cause alterations such as anoxia to sediment biogeochemistry due to increased sediment oxygen demand by microorganisms and fauna as well as benthic metabolism shifts to anaerobic processes such as sulfate reduction (Pearson and Rosenberg 1978). These changes inevitably lead to the classic benthic macrofaunal response to organic pollution: a community shift from one of diverse composition of epifauna and infauna (containing large, deep dwelling, bioturbating species) to a less diverse infaunal community with high abundances of small-bodied, shallow dwelling, opportunistic species such as the polychaete, *Capitella capitata* and anaerobic bacteria (Pearson and Rosenberg 1978).

Examples of this macrofaunal community succession have been found in areas of suspended bivalve aquaculture throughout the world. Tenore et al. (1982) compared benthic characteristics of two Spanish embayments (Rias de Arosa and de Muros) with floating raft mussel (*Mytilus edulis*) aquaculture, one of which (Arosa) produced more than half the total cultured mussel production of Spain (90,000–120,000 metric tons wet weight). Sediment organic matter concentrations in the Arosa ranged from 73% to 81%. Comparison of raft sites to non-raft sites in the Arosa showed lower species diversity and a 4-fold decrease in biomass at raft sites. Ria to ria comparison showed higher diversity and biomass (5–10x) in the less intensively cultured Muros. As well, the Arosa had both infaunal and epifaunal communities dominated by pioneering polychaete species as opposed to molluscs that were in the Muros. The authors concluded that these differences were most likely caused by the increased organic matter concentrations in addition to the high interstitial water content (~70%), which made the sediment unstable for many infaunal species (Tenore et al. 1982). In addition, increased abundances and biomass of invertebrate predators (large-bodied crab species and starfish), but not demersal fish, were found at raft sites compared to non-raft sites in the Arosa, but not the Muros. These differences were explained due to increased epifaunal densities and mussel fall-off in the Arosa, which increased prey for these predators. The lack of changes to the demersal fish community in the Arosa was explained by the decreased abundances of polychaetes, amphipods and small crab species, which are preferred by the dominant fish species, the goby (*Lesueurigobius friesii*).

Mattsson and Lindén (1983) recorded succession in benthic communities under three mussel culture sites in Sweden. The benthic community was sampled at five stations, three months following the set-up of a culture site with a faunal similarity index ranging from 74% to 82%. The community profile changed gradually as the original dominant species, which disappeared after 6 months, and was replaced by an opportunistic species apparently better adapted to the new benthic conditions. The remaining original species decreased successively (almost 3-fold decrease in Shannon-Wiener diversity index) and finally disappeared after 15 months. Three polychaete species (*Capitella capitata*, *Scolelepis fuliginosa*, and *Microphthalmus sczelkowii*), which prefer organically enriched sediments, became established as the predominate fauna under the culture sites. About 18 months after the mussels were harvested, the benthos had still not fully recovered to its original state. The effects on the benthic community were highly localized to an area of 5 m to 20 m around all culture sites sampled (Mattsson and Lindén 1983). It is important to note that these observations were made in the absence of a control site.

Kaspar et al. (1985) compared the transition in species composition under a mussel (*Perna canaliculus*) farm with a reference site 1 km away in Kenepuru and Marlborough Sounds, New Zealand. The reference site had a silty bottom with no large epifauna, whereas the culture site had clumps of mussels beneath the mussel lines, presumably broken off from the culture ropes. The authors noted an obvious difference between the composition of the epifaunal and infaunal populations at culture and reference sites. Greater species diversity was found at the reference site, where brittle stars, various bivalves, tunicates, sponges, crustaceans, and several species of polychaete worms were present. The infaunal community under the mussel lines comprised only polychaetes. The authors attributed this difference to mussel clumps providing substrates for numerous other organisms, which, in turn, attracted predators such as sea stars and a variety of fish. Similarly, a 39-fold difference in starfish (*Coscinasterias muricata*) density was also observed at *P. canaliculus* farms in New Zealand compared with unfarmed areas, and this change correlated to the abundance of living mussels on the seafloor (Inglis and Gust 2003).

Stenton-Dozey et al. (1999) examined the macrobenthic community (both infauna and epifauna) at a large (80 ha.) raft-culture lease of *M. galloprovincialis* in South Africa. From various unpublished sources, the authors reported sedimentation rates within the farm were 300 kg organic carbon $m^{-2}yr^{-1}$ (3x compared to outside). Significantly higher organic carbon and total reducible sulfur, along with significantly lower C/N ratios, were also reported from unpublished studies. In their own work, Stenton-Dozey et al. (1999) demonstrated seven of nine (78%) rafts sampled showed disturbance as compared to controls with macroinvertebrate dominance shifted towards polychaetes and scavenging gastropods. Carnivores were also noted to be attracted to the rafts as a result of mussel fall-off. Of all rafts sampled, those found nearest the lease center were the most disturbed. While the authors concluded sites were still disturbed after 4 years, diversity indices were beginning to show signs of recovery in some areas. However, when one of these rafts was re-examined in a subsequent study (Stenton-Dozey et al. 2001), the macroinvertebrate taxa was still dominated by detritivores (polychaetes) and carnivores and biomass was found to be 5% to 15% of that at reference sites. Sediment analyses also showed that particulate organic carbon was an order of magnitude higher than at a control raft and was accompanied by significantly higher total reducible sulfur.

In terms of macrofaunal community dynamics in areas of bivalve aquaculture, the general trend that emerges from the above studies is an increased rate of sedimentation and biodeposition supplemented by fall-off of cultured individuals, which increases organic matter loading to the benthos. In turn, changes to sediment geochemistry and particle size composition along with increased epibiont biomass favor succession to deposit-feeding species such as polychaetes and a subsequent attraction of large predators. As such, these results generally agree with the model proposed by Pearson and Rosenberg (1978).

Changes in meiofaunal density have also been observed at bivalve aquaculture sites. While decreased macrofaunal abundances were noted, Castel et al. (1989) also found a 2-fold increase in meiofaunal densities at a near-bottom (table) lease of Pacific oysters (*Crassostrea gigas*), relative to a control site. Conversely, Mirto et al. (2000) reported significantly lower meiofaunal density at a suspended mussel (species not given) longline lease compared with a control site 800 m away and Tenore et al. (1982) found no difference in meiofaunal abundance, diversity, and biomass among sites with and without raft culture of mussels in each of two bays (rias). However, meiofaunal abundances, diversities, and biomass in the latter study were lower than expected, perhaps reflecting some or all of increased organic matter sediment loads, sediment instability, or interactions with macrofauna. It is critical to note, however, that this study dealt with a sample size of only 2 bays and did not collect comparable data from bays without mussel aquaculture as a reference.

In addition to the meiofaunal changes noted, Mirto et al. (2000) also observed alterations of the microbial community at the same mussel lease in another component of the same study. Bacterial cell density increased 64% relative to the control site and a taxonomic shift in community structure to a higher proportion of cyanobacteria species was also recorded (Mirto et al. 2000). Similarly, Dahlback and Gunnarson (1981) observed the development of dense bacterial mats (*Beggiatoa* spp.) under mussel longlines while Tenore et al. (1982) also found increased abundances of bacteria at raft-culture sites versus non-culture sites in Ria de Arosa.

Bottom culture, with which bivalves are seeded on natural substrate, reared, and harvested by hand or mechanical means, has also been shown to influence sedimentation rates and benthic community dynamics (Ottman and Sornin 1985; Kirby 1994). Spencer et al. (1996, 1997, 1998) studied the physical and biological effects of plastic netting used for predator exclusion in Manila clam (*Tapes philippinarum*) culture. Experimental plots covered with netting with and without clams were compared to control plots. The presence of netting was found to increase organic matter concentrations and further increased sedimentation rates 4-fold which elevated the substrate profile 10 cm. This subsequently led to benthic community alterations that created a dominance of deposit-feeding worms. This condition was, however, reversible as the cultivation areas returned to conditions comparable to controls 12 months post-harvesting (Spencer et al. 1998). Ongoing research in Baynes Sound, British Columbia has also demonstrated that predator exclusion netting of Manila clam farms increased siltation (Bendell-Young, *unpub. data*). No data on recovery of leases in this region are available to date.

HYDRODYNAMIC INFLUENCE

In contrast to the above examples, some authors have found no negative effects of biodeposition from bivalve aquaculture on benthic sediment variables and/or communities (Baudinet et al. 1990; Grant et al. 1995; Crawford et al. 2003; Miron et al. 2005b). In each of these studies, it was speculated that local hydrodynamics may have played a role by advecting biodeposits away from the area immediately under the leases. Evidence supporting this has been found in studies by Chamberlain et al. (2001) and Hartstein and Rowden (2004). Chamberlain et al. (2001) examined multiple stations (separated by 20 m) along a transect set in the direction of dominant current flow through a *M. edulis* suspended culture lease in each of two bays of low hydrodynamic energy (current velocities of 2.85 and. 3.14 $cm.s^{-1}$ measured 2 m above the substrate) separated by 35 km. Total organic carbon, total nitrogen and percent composition of silt/clay of sediment samples were highest at the lease centre and declined with distance at the site with lower current velocity. Similarly, redox potential was lowest at lease center and increased monotonically with distance. Also at this site, significant differences in macrobenthic community structure and diversity were noted among stations. The station closest to the lease center had an impoverished community dominated by opportunistic polychaetes relative to the more diverse stations farther from the lease center along the transect (Chamberlain et al. 2001). Hartstein and Rowden (2004) examined suspended longline culture of mussels (no species given but most likely *P. canaliculus*) for differences in macroinvertebrate assemblages at sites. Samples were collected within and outside three leases in separate New Zealand bays; two relatively low-energy sites and one relatively high-energy site (mean current velocities of 3.29 and. 3.85 vs. 9.95 $cm.s^{-1}$). Significant differences in assemblages were found between samples taken within and outside leases at the low-energy sites, while no such differences were observed at the high-energy site. As such, these results appear to explain the conflicting results of some previous studies while providing further evidence current velocities may be suitable predictors of potential effects on benthos at bivalve aquaculture leases.

FAR-FIELD INTERACTIONS

In a study of 20 Prince Edward Island (PEI) estuaries, Shaw (1998) noted interesting results when comparing benthic geochemical and benthic community variables measured under leases, at "reference" areas within the same estuary, and areas in adjacent estuaries with no mussel culture. Water content, concentration of total sulfides, and percent organic matter of sediments were highest at leases but were not significantly different from reference sites in the same estuary. These variables were significantly lower at culture-free bays when compared with either leases or "reference" sites. In addition, abundance of benthic macroinvertebrate infauna and epifauna was nearly an order of magnitude higher at culture-free bays (Shaw 1998). Based on these results, it appears that suspended bivalve aquaculture may be imparting estuary-wide (or far-field) changes on benthic ecosystems. National or international comparison of the results is difficult as no other known published *in situ* studies have been conducted examining bivalve aquaculture interactions with benthos at this spatial scale with sufficient replication. However, recent work has attempted to provide more insight into this question by re-sampling the sites of Shaw (1998) with increased replication (more estuaries and more sites within each) and the addition of variables such as nutrient conditions, sedimentation rates, phytoplankton production and blooms, oceanographic conditions, and seabed mapping for the generation of models to predict ecosystem-level environmental effects and determine carrying-capacity (Dr. P. Cranford, Bedford Institute of Oceanography, Fisheries and Oceans, Canada, *pers. comm.*). As such, more data on this topic should be available in the near future.

PHYSICAL ALTERATIONS

Aside from hydrodynamic disruption, suspended bivalve aquaculture causes fairly limited physical disruption relative to bottom and near-bottom culture in intertidal and shallow subtidal areas (Pillay 2004). In addition to altering sedimentation processes these latter culture methods may influence benthic communities through substrate modification to enhance stability (leveling, graveling, fence installation), chemical and physical removal of predators and competitors, and disturbance associated with site maintenance and harvesting (personnel, vehicles, and machinery) (Jamieson et al. 2001).

Substrate enhancement

Modification of substrates by adding large volumes of gravel or crushed shells for cultch will alter benthic communities. At recently graveled mudflat and sandflat sites, Simenstad et al. (1991) compared epibenthic meiofaunal communities with control plots. The sandflat was found to have increased abundances and decreased diversity, whereas the mudflat had increased diversity. In comparing the newly graveled locations with each other, they were found to have significantly different assemblages, indicating the site-specificity of effects despite being manipulated in the same manner. Other studies on gravel enhancement have shown altered infaunal assemblages from dominance of deposit-feeding polychaetes to a community favoring bivalve species (Thompson 1995). While application of crushed shells as cultch is expected to modify habitats and benthic communities in the same manner as gravel (Kaiser et al. 1998), no known studies have been published on this topic.

Predator removal

Burrowing shrimp (*Neotrypaea* and *Upogebia*) act to destabilize sediments and smother bivalve species through their burrowing action (Simenstad and Fresh 1995). The insecticide carbaryl is employed to control shrimp in the Pacific Northwest of the United States and both lethal and sub-lethal effects have been reported on a suite of invertebrate and vertebrate species (reviewed by Simenstad and Fresh 1995). As chemical control measures are not used in Canadian bivalve aquaculture (Boghen 2000; Jamieson et al. 2001), this topic will not be addressed further. However, as noted by Jamieson et al. (2001), it is important that scientists and managers be aware of the effects of this compound as its use may be requested by growers as culture operations expand into areas not traditionally considered suitable for bivalve bottom culture.

While the physical removal of predators through trapping or hand-collection, occurs at aquaculture sites (Jamieson et al. 2001), there are no known studies of direct effects of this practice (as opposed to predator exclusion). However, it would be intuitive to expect increased prey densities in areas where this occurs. This is supported by the results of caging studies in natural habitats, which have demonstrated that exclusion of large epibenthic predators from sandflats results in increased bivalve density (Summerson and Peterson 1984).

Maintenance and harvesting activities

Evidence of physical disturbance due to equipment and personnel has been found at intertidal, near-bottom (trestle) oyster (*C. gigas*) culture in Ireland (De Grave et al. 1998). Samples taken under trestles, in adjacent access lanes, and at a control site 300 m away indicated decreased numbers of fragile, shallow-burying bivalves and small crustaceans and increased decapod abundance in the access lanes. In the absence of significant accumulation of organic matter, the authors concluded these changes were the result of physical disturbance from vehicle and foot traffic.

Many examples of effects of disturbance on benthic fauna by hand and mechanical harvesting have been reported. In Maine, commercial digging for soft-shell clams with a hoe caused a significant reduction in species richness and density of three polychaete species (Brown and Wilson 1997). Similar results were found in the Minas Basin of the Bay of Fundy where physical disturbance by commercial harvesting of bloodworms (by hand raking) and soft-shell clams (by digging) caused immediate reductions in biomass and abundance of intertidal benthic macro- and meiofaunal communities and a shift in community dominance from sessile, tube-dwelling species (spioniod and maldanid polychaetes) to mobile opportunists such as harpacticoid copepods, nematodes, capitellids, and mud shrimp (Westhead 2005). No data were collected on post-disturbance recovery of biota. Dolmer et al. (2001) also found similar results attributable to harvesting, whereby dredging a cultivated bottom during harvesting of mussels changed the community structure by reducing the density of small polychaetes. In Northern Europe, an immediate reduction in diversity and abundance of infaunal species in a muddy sand substrate occurred following the harvesting of Manila clams by a suction dredge. However, the invertebrate infaunal community returned to reference conditions after 12 months (Spencer et al. 1998). Similarly, Hall and Harding (1997) found high mortality of non-target benthic fauna with the use of suction and tractor dredges to harvest cockles (*Cerastostema edule*), but the fauna in disturbed sites recovered to that of controls within 56 days. While significant effects are often observed immediately following bottom-culture harvesting in unvegetated, soft-sediment habitat, this trend of quick recovery of invertebrate communities is also quite common (Kaiser et al. 1998).

Recovery of seagrass populations (most notably *Zostera* spp.), by contrast, is not so rapid. In some areas, such as the northwestern United States, eelgrass is removed from leases to increase local water circulation for bivalve feeding (Heffernan 1999). However, no studies have examined the influence of intentional eelgrass removals. Everett et al. (1995) showed significant decreases in *Zostera marina* density in areas of stake and rack culture of oysters in comparison to control plots. After one year, percent cover and shoot densities were significantly reduced at sites with both types of culture and *Zostera* was essentially eliminated from rack treatments at 17 months. These changes have been partially attributed to disturbance during set up and harvesting of both culture types combined with increased sedimentation at stake plots and increased erosion at rack plots (Everett et al. 1995). As well, the authors suggested these effects may have been due to benthic shading by the trestles (Everett et al. 1995). Two additional studies of stake and rack culture have demonstrated up to 75% reductions in eelgrass density (Carlton et al. 1991; Pregnall 1993). Peterson et al. (1987) found seagrass biomass fell by 65% below control levels following clam harvest with clam kicking boats, with a partial recovery after four years. It was also noted that hand-raking of unvegetated bottoms caused no direct effects relative to controls; however, raking of seagrass beds resulted in a 25% biomass decrease (Peterson et al. 1987). More evidence of culture effects on eelgrass has been reported by Waddell (1964). While no specific mechanisms are identified, comparison of oyster culture and reference plots demonstrated decreases in shoot density, shoot length, and biomass in culture plots with increased effects noted as time under culture increased. Biomass was reduced 30% after one year and 96% after 4 years with effects persisting up to two years post-treatment (Waddell 1964). Thus, it is evident bottom and near-bottom aquaculture practices have the potential for affecting *Zostera* beds. This is critical as disturbance of key habitats such as seagrass may have adverse effects on many species that use the habitat as a nursery ground (Kaiser et al. 1998). Despite this, no known studies have examined the effects on the population dynamics of such species (vertebrate or invertebrate) in areas where reductions in submerged aquatic vegetation have been attributed to aquaculture activities.

EPIBIONTS

The addition of cultured organisms and culturing structures invariably increases available substrate for both colonizing and free-living organisms (Spencer 2002). Tenore et al. (1982) have documented a diverse epibiont community of over 100 species dominated by small crabs, sea cucumbers, gastropods, lug worms, tunicates, and algae on floating mussel rafts in Spain. This increased biomass alters community structure, function, and productivity in the area of culture directly. As well, indirect influences via attraction of benthic invertebrate predators (Kaspar et al. 1985; Stenton-Dozey et al. 1999; Inglis and Gust 2003) and some demersal fish species (Chesney and Iglesias 1979) and subsequent diet shifts to epifaunal dominance have been noted (Lopez-Jamar et al. 1984; Freire et al. 1990; Fernandez et al. 1995; Freire and González-Gurriarán 1995).

Filter-feeding epibionts may further increase sedimentation of organic matter, which can enhance the previously described effects of biodeposition from cultured bivalves.

Potential support for this was found by Mazouni et al. (2001), who described increased abundance and diversity of ascidians on the lines of oyster culture racks in France and speculated their filter-feeding activity may significantly contribute to cultured bivalve biodeposition. As well, these authors noted increased abundances of *Capitella* spp. on culture lines as a result of sediment accumulation.

Increased epibiont density and abundance has also been found on predator exclusion netting deployed at bottom culture sites. Simenstad et al. (1993) and Bendell-Young (*unpub. data*) have both recorded increased algal cover while Spencer et al. (1996, 1997) have noted both increased periphyton (*Enteromorpha* spp.) and an associated increased density of grazing gastropods.

Increased available surface area for colonizing organisms by culture structures may also be aiding the spread of invasive species. In areas of Prince Edward Island, the club tunicate (*Styela clava*) and oyster thief (*Codium fragile tomentosoides*) have been reported in high densities at suspended mussel culture operations (ICES 2003). Densities of a related tunicate (*Ciona intestinalis*) in an affected lease in Nova Scotia were so high that a mussel farm was abandoned (ICES 2002). Much research is needed in this area as no known published studies have examined the potential effects of these invasive species on the structure and function of Atlantic Canadian benthic communities.

KNOWLEDGE GAPS AND RECOMMENDED RESEARCH

As detailed above, numerous studies have been conducted on bivalve interactions with benthic communities. However, these studies have focused almost exclusively on first-order relationships (abundance/density, distribution, and diversity). As such, little is known of the influence of bivalve aquaculture on second-order relationships such as growth or reproduction of ecologically and/or commercially important species. Work in this area has begun through ongoing examinations of the influence of suspended blue mussel culture on the growth rates of juvenile winter flounder in Prince Edward Island (C. McKindsey, *pers. comm.*). Studies such as this will provide needed insight into hypotheses of potential positive influences of bivalve culture on secondary productivity. However, more resources need to be invested in supporting studies to gain a better appreciation of this aspect of bivalve culture.

Related to this, studies of the interactions of bivalve aquaculture with benthic primary producers, especially seagrass communities, are surprisingly lacking. Given their ecological role in processing coastal nutrients and as critical habitat and nursery grounds for many species, more study on this issue is warranted. In general, the influence of bivalve culture on these communities has been found to be negative as bottom and off-bottom cultures are generally found in intertidal and shallow subtidal zones where seagrass is almost exclusively distributed. In contrast, suspended blue mussel culture generally occurs in deeper waters outside of normal range of temperate seagrass distributions, thus almost entirely negating the necessity for studies of interactions. This situation has made it difficult, if not impossible, to separate interactions as a result of physical disturbance from those of biodeposition. However, with the recent increases in the prevalence of suspended oyster aquaculture in the shallow subtidal zones of eastern New Brunswick, the opportunity to examine the potential influence of bivalve biodeposition of seagrass population and community dynamics has arisen. Specifically, hypotheses addressing growth rates and distributions of seagrass at near-field and far-field scales should be tested to provide information for resource managers to effectively protect these areas without unnecessarily hindering the development of this burgeoning industry.

In addition, almost all of the studies in this review have focused on local (near-field or footprint) effects, with reference sites often selected within the same bay. As the results of Shaw (1998) demonstrate, this may be interfering with our ability to detect change when it actually occurs. Therefore, the spatial scale of resolution on which research questions are based needs to be expanded from the lease-scale to address hypotheses of estuary/bay-wide ecological changes to structure, function, and productivity of benthic communities, focusing on these entire systems as replicates. To date, no published scientific studies from this perspective have been found.

Finally, despite the fact that coastal and estuarine systems worldwide are influenced by multiple sources of anthropogenic enrichment (municipal wastewater processing, fish processing plants, agricultural inputs, pulp and paper effluents, etc.), no published studies were found addressing the potential for cumulative effects of these influences and bivalve aquaculture on benthic ecosystem changes. In the face of rising cultural and scientific awareness of eutrophication of coastal areas (Cloern 2001), research examining the relative contribution of each of these inputs to observed benthic community changes is desperately needed for the development of effective management plans with holistic perspectives.

PREDATOR EFFECTS RELATED TO BIVALVE CULTURE

Most research on interactions between predators and cultured bivalves has studied the effect of predators on mollusc aquaculture, rather than the effect of aquaculture on predators and their prey. In fact, most have focused on methods of control or exclusion of predators (Furness 1996; Edwards 1996; Spencer 1992; Wilson and Brand 1994; Beattie 1995; Summerson et al. 1995; Barbeau et al. 1996; Powell et al. 1997; Avault 1998; Nadeau and Cliché 1998; Barbeau and Caswell 1999; Walton et al. 1999). Most of the studies on predator control evaluate techniques (e.g. fencing; netting; substrate modification; seeding size) employed to minimize the affect of predators on cultured species, however, they do not consider their effect on predator populations. To our knowledge there are very few, if any, studies that evaluate the effect of these techniques on predator populations.

In Atlantic Canada, seabirds are the most important "pelagic" predator in mollusc aquaculture (Thompson 1998–1999), while crabs and sea stars are the most important benthic predators (Miron et al. 2005a). Certain species of lobsters, gastropods, worms, and fish are also significant predators. Although the number of predatory species is quite small, the abundance of individuals may often be sufficiently high to incur substantial mortalities (Spencer 1992). Reducing predator densities before seeding is considered the most effective tool to increase the cultured species survival (Spencer 1992; Wilson and Brand 1994; Barbeau et al. 1996; Barbeau and Caswell 1999); however, few studies have looked at the ecological effect of such activities.

In some instances, aquaculture activities seem to have an effect on predator density and distribution. Studies have found predators aggregating near bivalve seeding sites (Volkov 1985; Wilson and Brand 1994). Dense aggregations of starfish consuming mussels that had dropped off were observed beneath mussel rafts in Ireland (Rodhouse et al. 1985). The same predator aggregation response has been observed in infaunal communities. Dense aggregations of a predatory nemertean were observed in a newly seeded soft-shell clam (*Mya arenaria*) area where none were present before the bivalve introduction (Rowell and Woo 1990). In a study on the interaction between oyster culture and predatory birds, Hilgerloh et al. (1999) found that although the number of species was not significantly different, the densities of some species were greater, supporting the aggregations theory. It is, however, unclear whether these predators were immigrants or aggregations of local populations. Barbeau et al. (1996) studied the dynamics of predators in relation to scallop enhancement and found that temporal variation in abundance and spatial distribution of sea stars (*Asterias vulgaris* and *A. forbesi*) and rock crab (*Cancer irroratus*) did not correlate with seeded sea scallops (*Placopecten magellanicus*). Studies on seeded juvenile sea scallops concluded that high mortalities due to predation did not increase aggregation of predators, but increased consumption rates of predators already located in the seeding area (Barbeau et al. 1994; Barbeau et al. 1998; Wong and Barbeau 2003). Existing studies do not clearly indicate whether the predator populations are being increased or just being concentrated in these areas. However, a study looking at changes in rocky subtidal communities showed that sea star recruitment was positively related to a significant increase of mussel prey the previous year (Witman et al. 2003). The same type of response could be possible in an aquaculture setting since structures such as mussel seed collectors provide a settlement substrate as well as a food source for juvenile sea stars (Murray MacKinnon et al. 1992–1993). Nevertheless, most bivalve predators have larval phases to increase their dispersal. Therefore, in order to increase local predator populations, the water system would need to have high larvae retention. At this time no clear evidence has shown a relationship between increased prey densities due to aquaculture activities and predator population abundance in the surrounding area. There are no known long-term studies on the dynamics of predator-prey communities in relation to mollusc aquaculture (M. Barbeau, personal communication).

KNOWLEDGE GAPS AND RECOMMENDED RESEARCH

More research is required on the interactions between cultured bivalves and predator abundance and distribution. The studies should cover a wide geographical area to determine the effect on overall productivity of cultured species and other prey species.

Research on the effect of the methods of predator control on targeted and non-targeted species is also needed. More information on the effects of altering the abundance of various cultured species, by seeding or harvesting, on predator and prey communities would also be very beneficial to understanding cultured bivalve and predator interactions.

EXOTIC SPECIES RELATED TO BIVALVE AQUACULTURE

There has been much discussion and debate about the importance of aquaculture as a vector for the introduction and spread of exotic species, defined here as a species that has been introduced to an area outside of its natural range (Carlton 1992a, 1992b; Naylor et al. 2001; Streftaris et al. 2005). However, to our knowledge, there has yet to be a thorough review of the importance of bivalve culture in particular, or aquaculture in general, to the introduction and spread of exotic species (but see Carlton 1992b).

There are two broad classes of introductions that may result from bivalve aquaculture. First, there is the establishment and spread of non-endemic species that have been intentionally introduced into an area for aquaculture purposes, the "target" species. Classic examples of this include the establishment of the Pacific oyster (Crassostrea gigas) on the Pacific coast of North America (Ruesink et al. 2005) and of the Mediterranean mussel (Mytilus galloprovincialis) in South Africa (Branch and Steffani 2004). Second, there is the establishment and spread of species that are associated with the introduced bivalves (Carlton 1989, 1999). These species may include both "hitchhiking" species – animals and plants that grow in association with the bivalves – and diseases that may cause outbreaks in the same or other species (Barber 1996). This acts at two spatial scales: at an inter-regional or international scale with respect to the initial introduction of hitchhiking species, and also at a regional scale, where the transfer of stock among sites may be very important to the spread of established exotic species locally (Bourque et al. 2003a). Other related vectors such as processing plants for bivalves are also of importance at a regional scale. The provision of novel habitat by the cultured species may also allow for the establishment or amplification of exotic species that may be introduced through other vectors or of native species that thrive in the new habitat (Carver et al. 2003; Rodriguez 2005).

This portion of the SOK reviews the relations between bivalve aquaculture and the introduction and spread of exotic species associated with bivalve aquaculture, including the exotic bivalve species themselves that are being cultured, and their effects on the environment. It should be noted that the majority of the existing literature addresses the issues as they relate to oyster culture, probably because this appears to be the single greatest vector for all types of introductions (planned or otherwise) in bivalve aquaculture (Carlton 1992b). There is little published information about other bivalve species with respect to their role as exotic species or as vectors for other exotic species. The following discussion is thus largely based on oyster-oriented literature but has been expanded where possible to include other taxa.

HISTORY OF EXOTIC BIVALVE INTRODUCTIONS FOR AQUACULTURE AND THEIR ROLE AS VECTORS FOR OTHER EXOTICS

Bivalves have been grown and introduced for culture throughout the world for hundreds of years (Mann 1983; Chew 1990). The first records of bivalve transfers date back to at least 1714 in Europe for oysters (Wolff and Reise 2002). In North America, serious efforts to introduce exotic species of bivalves for culture started on the west coast with the attempted introduction of *Crassostrea virginica* in Puget Sound in the 1870s and 1880s and continued until the 1920s, and in British Columbia from the 1880s until the 1930s (Wonham and Carlton 2005). Effort was subsequently directed towards introducing *C. gigas* on the west coast, with an initial attempt in Puget Sound in 1875 and continuing efforts there starting from 1902 onwards, and in British Columbia starting in 1912–1913 (Wonham and Carlton 2005). Many attempts have been made to introduce the European flat oyster (*Ostrea edulis*) to both coasts, starting in 1949–1961 in the eastern United States and 1957–1959 in eastern Canada, and on the west coast following this (Chew 1990; Carlton 1992a; Shatkin et al. 1997; Vercaemer et al. 2003; Ruesink et al. 2005).

Although there have been sporadic efforts to introduce non-indigenous bivalves to eastern Canada for aquaculture purposes, the bivalve aquaculture industry there is based largely on endemic species (Boghen 1995), including mussels (*Mytilus edulis* and *M. trossulus*), *C. virginica*, and the Giant and Iceland scallops (*Placopecten magellanicus* and *Chlamys islandica*, respectively) although there is also limited culture of *O. edulis*, and the bay scallop (*Argopecten irradians*). Consequently, introductions associated with bivalve aquaculture are relatively scarce in the general area (Carlton 1999). In contrast, the aquaculture industry on the west coast of Canada is based largely on non-indigenous species. For example, the oyster aquaculture industry on the west coast of North America, including British Columbia, is based largely on a non-indigenous species, the Pacific oyster, *C. gigas* (Quayle 1988). Introductions of this species, and to a lesser extent of *C. virginica* and other oyster species, outside of their native range for aquaculture have been suggested to be one of the greatest single modes of introduction of exotic species worldwide (Wasson et al. 2001; Ruesink et al. 2005). For example, transfer of organisms with bivalves has been suggested to be the most important source of exotic species in northern Europe (Minchin 1996; Streftaris et al. 2005) and among the most important vectors elsewhere in that continent (Ribera Siguan 2003; Streftaris et al. 2005). In the northeast Pacific, some authors suggest that oyster introductions have even been the major source of introduction of exotic molluscs (Carlton 1992a) and invertebrates in general (Wonham and Carlton 2005), historically contributing at least as many of the exotic species in that area as has international shipping. Ironically, the intentional introduction of *C. gigas* to the west coast of North America also likely resulted in the introduction of the manila clam (*Tapes philippinarum*), currently the most important infaunal clam species that is cultured in British Columbia (British Columbia Shellfish Growers Association 2005). Other non-indigenous species being cultured in British Columbia include the Mediterranean mussel (*M. galloprovincialis),* the blue mussel (*M. edulis*), the European oyster (*O. edulis)*, the Kumamoto oyster (*Crassostrea sikamea*), and the Japanese scallop (*Patinopecten yessoensis*), with efforts underway to evaluate the culture potential of the varnish clam (*Nuttallia obscurata*).

EXOTIC BIVALVES AS HABITAT, COMPETITION WITH ENDEMIC SPECIES, AND ECOSYSTEM EFFECTS

The general role of cultured bivalves in the ecosystem is covered in other sections of this SOK and will not be addressed further here. That being said, as all the bivalves currently being cultured to any major extent are engineering species (Jones et al. 1994 – species that modulate the availability of resources to other species by causing physical state changes in biotic or abiotic materials and thus modify, maintain or create habitats), the effect of exotic bivalves in culture on the ecosystem may be considerable if they expand their range beyond the limits of the culture sites. In fact, some modeling work (Cuddington and Hastings 2004) suggests that such invasive engineering species may have the greatest effects on the receiving ecosystem.

The ability to predict whether an exotic bivalve that has been introduced into an area will establish, propagate and spread is an inaccurate art (Shatkin et al. 1997; Ruesink et al. 2005), much as it is in general in invasion biology (Lodge et al. 1998; Ricciardi and Rasmussen 1998; Heger and Trepl 2003). In short, the ability of a given species to establish is a function of how well the environment in which it finds itself provides for its needs for food, reproduction and habitat, including interspecific interactions with the local flora and fauna and abiotic factors. Its ability to spread will depend on its dispersal ability and the amount of available suitable habitat.

Bivalves, especially large, colonial forms like those grown in aquaculture, may have a considerable influence on the ecosystem (Crooks 2002) and their effect may extend beyond the communities of exotic bivalves themselves and into adjacent habitats (Dame 1996). According to Ruesink (2005), their effect may be greatest in soft-sediment environments where species such as oysters may provide considerable hard substrate, effectively changing a soft-bottom system to a hard-bottom one, with the concomitant increase in physical heterogeneity, provision for attachment for sessile species, hiding spaces for mobile ones, etc. Surprisingly, few studies have studied the effect of exotic bivalves that have spread from aquaculture sites on the environment and even fewer have done manipulative experiments.

The influences of introduced bivalves on benthic communities that lack such engineering species are pretty much as would be expected from the ecological literature. In general, the addition of exotic oysters to soft-sediment areas leads to an increase in the abundance of most groups of organisms. In one of the rare manipulative experiments to evaluate the influence of an introduced bivalve, Escapa et al. (2004) showed that the presence of intertidal *C. gigas* beds increased the abundance of both infauna and epifauna as well as that of birds relative to adjacent control areas without oyster beds. Similarly, observational studies done in Washington State (Dumbauld et al. 2000; Hosack 2003, cited in Ruesink et al. 2005) have shown that the diversity and abundance of various groups of organisms in mud flats are increased by the presence of *C. gigas* beds. The influence of exotic oysters on hard substrate-associated species is variable and often indirect. For example, *C. gigas* on rocky coasts in British Columbia tends to occupy the high intertidal zones and, far from limiting the abundance of the normal barnacle community in that zone, actually increases the surface area for the barnacles (Bourne 1979, cited in Ruesink et al. 2005). *C. gigas* has also been observed to recruit to mussel beds on both rocky coasts (Orensanz et al. 2002) and mudflats (Wolff and Reise 2002), slowly transforming the former mussel beds into oyster reefs.

Although often understandable in hindsight, the influence of exotic bivalves on the functioning of the benthic and/or intertidal ecosystem is very hard to predict. Branch and Steffani (2004) provide an excellent review of one case (*M. galloprovincialis* in South Africa). In short, their findings suggest that although some of its effects may be predicted with good information on the local biology and ecology, some are only understandable in hindsight as the diversity of interactions the mussel has with the local fauna and the environment make it difficult to predict all potential effects.

Properties that allow the establishment and spread of invasive species include rapid growth under a range of environmental conditions, great physiological tolerances, and great reproductive output (Ruiz et al. 2000; Cox 2004). These are among the same attributes that are sought out for aquaculture species (Anonymous 2004; Branch and Steffani 2004). In general, interactions between introduced species and native congeners or their approximate ecological bivalve equivalents (e.g., mussels and oysters) differ in their environmental requirements such that strong competitive interactions between them may be limited. That being said, Ruesink et al. (2005) list many examples of oyster species with overlapping habitat requirements and show that exotic oysters consistently outgrow and basically dominate endemics. The same is true for mussels. Branch and Steffani (2004) show how the introduced *M. galloprovincialis* has largely replaced one of the endemic species of mussels (*Aulacomya ater*) on rocky coasts in South Africa as the two species overlap greatly in their basic life requirements but that the rates of growth, reproductive output, tolerance to stress, disease resistance, and survivorship are greater for *M. galloprovincialis*. In contrast, the two other sympatric mussels, *Perna perna* and *Choromytilus meridionalis*, are much less affected as their basic life requirements differ from those of *M. galloprovincialis*.

The importance of an introduced species replacing an endemic one on the functioning of the benthos depends on how ecologically similar the different species are. Different species, even within the same groups, are not ecological equivalents. For example, with respect only to physical structure, neither *C. gigas* nor *Crassostrea ariakensis* form on the expansive high-relief reefs as does *C. virginica*. So, although either of these non-endemic species may in some way replace the filtration capacity and nutrient cycling services that *C. virginica* normally provides, neither would be able to provide the ecological services associated with this trait of *C. virginica*. Similarly, many authors (Suchanek 1979, 1981, 1985; Seed and Suchanek 1992; Iwasaki 1994, 1995; Seed 1996) have shown that different species of mussels differ greatly in the type of 3D structure they create in the natural habitat (e.g., mono-layers vs. multiple layers of mussels, different densities of byssus and mussels, different sizes, etc.) and thus would likewise alter any system in which they replaced local species, as is occurring in South Africa (Griffiths et al. 1992).

Dense concentrations of bivalves also have the potential to significantly influence water column and water column-benthic interactions (Gosling 1992; Dame 1996). However, as pointed out for the benthic processes, different bivalves differ in how they do this and thus the addition or replacement of a similar bivalve by the expansion of an introduced bivalve species may have complex cascading effects on water column and nutrient dynamics. Such interactions remain largely unstudied to date.

EXOTIC HITCHHIKERS

There are a number of ways in which exotic species may be introduced into a new environment when bivalves are transferred for aquaculture. Exotics may be present within the bivalves, on the bivalves, in water or on equipment (such as ropes, socking material, cages) transferred with the bivalves, within sediment transferred within empty shells of dead individuals, or associated with other hitchhiking species. The importance of the different modes of transfer varies with the different exotics and some may or may not be effective.

There are three major classes of exotic hitchhikers of concern with respect to bivalve aquaculture and introductions and transfers: exotic macrospecies including algae and animals, exotic phytoplankton (toxic and otherwise), and exotic disease species. Each of these may influence the bivalve species being cultured or the surrounding ecosystem. At the time of writing, there are a number of worrisome invasive species associated with bivalve culture in Canada. These include the suite of invasive ascidians that is plaguing the mussel industry in Prince Edward Island (the solitary tunicates *Styela clava* and *Ciona intestinalis* and the colonial species *Botrylloides violaceus* and *Botryllus schlosseri*, known commonly as the clubbed, vase, violet, and golden star tunicates, respectively) and another species that is fouling bivalve culture sites in British Columbia, *Didemnum* sp., which has also been reported off the coast of Nova Scotia. Other macroscopic species of concern include the green crab (*Carcinus maenas*) the skeleton shrimp (*Caprella mutica*) and the green alga (*Codium fragile* ssp. *tomentosoides*) There are also a number of worrisome disease organisms, mostly associated with oyster culture, including MSX disease (Burreson and Ford 2004) and *Bonamia ostreae* in European flat oysters (Bower and McGladdery 2003). Although all these species may not necessarily have been introduced initially with bivalve aquaculture, they do seem to be associated with it and thus bivalve culture may play an important role in their secondary spread. Each may also have significant effects on both the bivalves in culture and in the general local environment.

EXOTIC MACROSPECIES

Exotic macrospecies of algae and invertebrates may affect the bivalves that they are associated with in culture and the environment in general once introduced along with bivalves for aquaculture. Once again, it must be pointed out that the literature dealing with this subject is quite limited and much of the available information is only available in the "grey literature," including reports and conference proceedings.

The most obvious effect of exotic macrospecies on aquaculture is the fouling of the bivalves that are being cultured and the gear (lines, cages, buoys, etc.) used to do this. The tunicates and others listed above are classic examples from Canada (and elsewhere for some species). It has been suggested that at least some of these tunicates have been introduced and/or spread through bivalve aquaculture (Lambert and Lambert 1998). Fouling organisms such as tunicates likely compete directly with bivalves in culture for food and space, potentially reducing growth rates and increasing stress and mortality (Lesser et al. 1992; Bourque et al. 2003a; Carver et al. 2003). That being said, different filter feeders, both bivalves and the fouling tunicates, feed on different types of food such that competition between mussels and tunicates is species-specific. For example, *S. clava* and *M. edulis* feed on about the same food (Bourque et al. 2003b) whereas *C. intestinalis* and *M. edulis* feed on different sizes of food (Lesser et al. 1992). Under the latter scenario, Lesser et al. (1992) suggest that the mussel and fouling species are not likely strong competitors for food and that the latter should not influence mussel yield unless food is a limiting factor. However, this idea does not take into account the simple physical barrier that the tunicates create, which may reduce the availability of food to the mussels underneath. The presence of such large filter-feeders may also filter out large quantities of food and potentially change the local carrying capacity of a given area for bivalve culture. The presence of such abundant and large macrospecies in bivalve culture operations also greatly affects general operations within the culture sites and for processing as all the lines, etc. used are all much heavier and the tunicates tend to gum up the processing equipment.

The green crab is also of concern for bivalve aquaculture in Canada. *C. maenas* is a voracious eater and seems to particularly like bivalves (Behrens Yamada 2001). On the east coast of North America, it has been blamed, in part, for the decline of the soft-shell clam population (Glude 1955). The bourgeoning soft-shell clam aquaculture industry in the Gulf of St. Lawrence is thus under threat from this species. Floyd and Williams (2004) suggest that farmers will have to protect the young clams until they reach a size at which they are no longer vulnerable to the crab. As the crab has also been observed in southern British Columbia in recent years (Jamieson 2002), the species is also likely to be of concern to the infaunal clam industries on that coast as well. Although green crabs are not known for its climbing ability, it is also common on mussel lines and scallop cages in areas where it is widespread (McKindsey, personal observations) and thus may also have an effect on these. The invasive skeleton shrimp (*C. mutica*) seems to be widespread in the southern Gulf of St. Lawrence and is thought by some farmers to be responsible for a decline in mussel spat-fall in Canada and elsewhere (Cook et al. 2004). Once again, little or no research has addressed these points.

The transfer of bivalves is also a well-known and important vector for macroalgae (Rueness 1989; Neushul et al. 1992; Ribera Siguan 2003; Mineur et al. 2004). In eastern Canada, the green algae *Codium fragile* ssp. *tomentosoides* (hereafter, *Codium*) is one such species. *Codium* is thought to have originally been transferred to northeastern North

America via oyster culture (Malinowski and Ramus 1973) and to Atlantic Canada with shellfish from the United States (Campbell 1997). Currently it is found in Nova Scotia, New Brunswick and Prince Edward Island (Hubbard and Garbary 2002) and in the Magdalen Islands, Quebec (Simard et al. in press) and often in association with bivalve aquaculture. Bivalves on which *Codium* grows are often dislodged because of the increased drag they impart to the animals (Trowbridge 1998). The alga has also been shown to smother blue mussels and bay oysters in eastern North America by attaching to the valves of the animals and keeping them shut (Fralick 1970, cited in Trowbridge 1998) and may also render afflicted bivalves more susceptible to predation (Ramus 1971). Afflicted bivalves may also have lower meat yields (Galtsoff 1964, cited in Trowbridge 1998) and presumably growth rates. Thus, it is a concern for bivalve culture operations. Hanisak (1979) suggests that *Codium* may be nitrogen-limited for a good part of the growing season. Bivalves increase the concentration of nitrogen-based compounds in the water directly through excretion and indirectly through mineralization of settled pseudofeces and feces in the surrounding sediments (e.g., Prins et al. 1998), this being particularly true in aquaculture situation (Dame 1993). Thus, it is reasonable to predict that association with bivalves in culture may increase the growth and productivity of *Codium* in some sort of cascading effect.

All the species associated with bivalve culture discussed thus far may also have an influence on the surrounding ecosystem. However, the importance of the suite of tunicates on the surrounding ecosystem is not well studied. Further, when they have been studied, they have usually been investigated as a part of the surrounding ecosystem, not as an influence on it (Osman and Whitlatch 1995b, 1995a, 1995c; Stachowicz et al. 1999; Stachowicz et al. 2002; Osman and Whitlatch 2004), although there have been some exceptions (Whitlatch et al. 1995). The influence of these species on the ecosystems in PEI may be greater than they seem to be further south in New England. Observations in numerous embayments in PEI have shown *B. violaceus* overgrowing eelgrass (*Zostera marina*) and various algae in the areas where it is prevalent in mussel farms and it has also been observed (A. Locke, personal communications) on a large proportion of the rock crabs (*Cancer irroratus*) in the two embayments that were examined in 2005. The influence of hitchhikers on the functioning of the ecosystem may be considerable. For example, Cloern (1982) suggests that, together, three exotic bivalve species (*Tapes philippinarum*, *Gemma gemma*, and *Musculista senhousia*) that arrived with oyster introductions (Carlton 1992a) may filter the entire volume of water of South San Francisco Bay within one day. Similarly, the slipper shell (*Crepidula fornicata*), originally introduced into England with *C. virginica*, has had great effects on some benthic communities in Europe, particularly in France (see recent review by Goulletquer et al. 2002), where it has displaced important commercial bivalves, such as the great scallop (*Pecten maximus*) in some areas (Chauvaud et al. 2003), but has had little effect elsewhere (De Montaudouin et al. 2001).

EXOTIC TOXIC AND NUISANCE PHYTOPLANKTON

Although historically thought to be largely associated with introduction from ballast water (Simard and Hardy 2004), the importance of shellfish introductions to the introduction and spread of phytoplankton that cause harmful algal blooms (HABs) and other detrimental ecosystem effects is now being recognized (Kaiser and Beadman 2002). A number of studies have shown that phytoplankton may be transported via the transfer and introduction of bivalves for aquaculture. Although any stage may be transferred, the concern may be greatest for the resting stages (spores and cysts) as these are the most robust.

Toxic and other nuisance phytoplankton may obviously be transferred with water or as cysts or other resting stages in sediments in bivalve transfers; however they may also be transferred on the external surfaces of bivalves (Minchin 1996). For example, Lawrence et al. (2000) studied the relationship between macroalgae and mussel farming and found the toxic (responsible for diarrheic shellfish poisoning, DSP) dinoflagellate *Prorocentrum lima* growing associated with the brown algae *Pilayella littoralis* that was growing on mussels and equipment in Nova Scotia. Interestingly, *P. littoralis* grew quicker on mussel lines than on control mussel lines with dead mussels. So, there may be some feedback whereby excretion from the mussels in culture stimulate the growth of the macroalgae, as was suggested for *Codium* above, and thus also the toxic phytoplankton species. Following a DSP outbreak, Levasseur et al. (2003) studied the abundance of the dinoflagellate *Prorocentrum lima*, the presumptive causative species for the observed DSP associated with mussel socks from two culture operations in separate lagoons in the Magdalen Islands, Quebec. They found this species and a further previously unobserved congener, *P. mexicanum*, associated with the epibionts growing on the socks and in the guts of the mussels. Both these studies show that *P. littoralis* may indeed live in association with mussels in culture and thus may be transferred along with mussels during stock transfers.

A number of studies has also shown that phytoplankton may also be transferred internally along with bivalves with stock transfers. Laing and Gollasch (2002) discuss how the nuisance diatom *Coscinodiscus wailesii* may have been transferred to Europe by oyster importations, with it possibly having been transported within the gut or pseudofeces of oysters in the form of resting cells. Similarly, Tsujino et al. (2002) found abundant viable cysts of the toxic dinoflagellate *Alexandrium* spp. in fecal pellets of bivalves in Japan, thus suggesting that this genus may also be transferred with bivalves for aquaculture purposes. This was further supported by work by Bricelj et al. (1993) who showed that the feces of *M. edulis* can contain viable *Alexandrium fundyense* cells and Hallegraeff (1993) has reported resistant resting stages from the digestive tracts of bivalves. Upon dissection of numerous mussels following an outbreak of paralytic shellfish poisoning (PSP), the potentially toxin-producing dinoflagellates *Gonyaulax excavata* (*Alexandrium tamarense*) and *Prorocentrum minimum* were found on the gills and in the digestive tract of mussels from areas where the suspect mussels originated (Langeland et al. 1984). In perhaps the most complete study of its kind, Scarratt et al. (1993) did an experiment to determine the potential of *A. tamarense* being transferred with scallop (*P. magellanicus*) and mussel (*M. edulis*) spat. The study showed that live cells were released from the bivalves after spending 6 hours under simulated transfer conditions. Subsequent work has shown how these and other species of phytoplankton may all pass through a variety of bivalve species and remain viable (Laabir and Gentien 1999; Bauder and Cembella 2000;

Harper et al. 2002; Springer et al. 2002; Hégaret et al. 2006). This work highlights the possibility of introducing toxic or otherwise harmful phytoplankton with bivalve introductions.

EXOTIC PARASITES AND DISEASES

Diseases in many species of bivalves in culture and in fisheries are well known throughout the world (Harvell et al. 1999, see also the special issue on bivalve diseases in Aquatic Living Resources 17(4) 2004). In fact, as pointed out by Figueras (2004: 395), "bivalve diseases are one of the critical bottle necks causing important and recurrent losses in bivalve culture." Thus, with respect to diseases of oysters, both Farley (1992) and Ruesink et al. (2005) suggest that most mass mortalities have resulted from the transfer of infectious stock. Indeed, it has been suggested that one of the more infamous bivalve diseases in Canadian history, the outbreak of Malpeque Bay disease in oysters in Prince Edward Island in 1915, resulted from a transfer of *C. virginica* stock from New England (Barber 1996). That being said, many diseases have only recently been described, are cryptic and may not become expressed once an introduction has taken place (Minchin 1996). In general, species of concern fall into one of 4 main taxa: viruses, bacteria, protozoans, and higher invertebrates. Good general reviews of the main species in eastern Canada are available from Fisheries and Oceans Canada (2001) [please see query #8]and Bower et al. (1994), and Bower and McGladdery (2003) provide a more in-depth discussion about all the major species. Good reviews for pathogens of oysters and their effects may be found in Shatkin et al. (1997), Anonymous (2004), and Ruesink et al. (2005).

MANAGEMENT ISSUES

From the above, it is clear that the introduction and transfer of bivalves for aquaculture purposes is a major source of introduction of exotic species. Although not extensively studied, it is also clear that such interactions may have profound effects on bivalve culture itself and also on the receiving ecosystems. It is also abundantly clear that once established, exotic species are rarely eliminated from their new habitat (Mack et al. 2000). Thus, exotic species must be checked before they arrive in a new area. Appropriate governance must be established to ensure that risks of introductions are minimized.

Risk assessment

The first line of defence lays in completing effective risk assessment for any proposed stock transfers (Rosenfield 1992; Minchin 1996; Minchin and Rosenthal 2002; Wolff and Reise 2002; Anonymous 2004; Forrest et al. 2004; Ruesink et al. 2005). At this time, most approaches internationally are based loosely on the ICES Code of Practice on the Introductions and Transfers of Marine Organisms (ICES 1995). In short, the Code gives a flowchart to follow to ensure that the chances of introductions are minimized. The following chart is summarized from Ruesink et al. (2005) and ICES (2005) and emphasizes the need for 5 main steps:

1. An extensive understanding of the functioning of the receiving ecosystem (predator-prey interactions, competition, diseases, environmental responses, etc) and of the basic requirements of the target bivalve species. Use this information for steps 2–4, below.

2. Determine the probability of (i) colonization and establishment of the target bivalve species in the target area, and (ii) the potential for the bivalve to spread.

3. Estimate the impact of the introduction of the target bivalve species on the receiving ecosystem, including trophic interactions, habitat transformations, and interactions with native species of concern (threatened or declining).

4. Estimate the probability of establishing a pathogen or parasite or other deleterious organism into the receiving ecosystem. Although not explicit in the Code, this step should also include any potential impacts of all possible hitchhiking species.

5. Establish quarantine and disinfection protocols to help prevent the introduction of undesirable hitchhikers, possibly with the release of only proven uncontaminated progeny into the environment, and the development of a contingency plan to withdraw the species should this become necessary.

It should be stressed that the information required in step 1 is rarely available (Branch and Steffani 2004). That being said, the identification of crucial knowledge gaps in this step is a logical way to identify the most pertinent research. Several case studies are available (ICES 1995; Anonymous 2004; Ruesink et al. 2005) that show the process fairly well. Orr (2003) outlines a more general risk analysis process for aquatic organisms.

It is important to note that establishing such regulations does seem to help curb the influx of exotic species in a given area. Prior to about 1960, the ecological implications of large-scale introductions of exotic bivalves were largely ignored; transfers, etc. occurred without much foresight (Wolff and Reise 2002). Since then, many codes of practice have been implemented with respect to shipping, bivalve transfers, etc., and there has been a concomitant decrease in the rate of exotic species introductions, at least in Europe (Streftaris et al. 2005). While transfers are thus less important to the introduction of novel species today they are still important on a regional scale both within Europe (Wolff and Reise 2002) and eastern Canada (Bourque et al. 2003a). In contrast, when such logic is not followed, unwanted introductions may occur. A good example of this concerns *Mytilicola orientalis*, a parasitic copepod from Japan that occurs in the lower intestine of oysters and mussels. Britain and Ireland were initially free of the parasite because of historic quarantines for *C. gigas*. However, a EU directive to allow half-grown oysters to be transferred from France to Ireland led to the introduction of the parasite there

(Minchin 1996; see also Minchin and Rosenthal 2002 for other effects of the EU directive).

Caveats with respect to spread and predictions of ecological effects.

Predictions of the risk of spread of introduced bivalve species for aquaculture and of ecological effects are only as good as the information upon which they are based. Although the requirements of the bivalves being introduced are usually fairly well known, this is certainly not always the case. Further, novel interactions within a new environment may also limit the accuracy of predictions based solely on information from elsewhere. For example, although the *C. gigas* culture industry in Tasmania, Australia, is entirely based on hatchery-raised seed, the species has been declared a "noxious fish" further up the coast in New South Wales, where it has escaped from the hatchery-based system and spread, affecting the locally important Sydney rock oyster (*Saccostrea commercialis*) industry (Shatkin et al. 1997).

Similar caveats with respect to the ecological effects of introductions on the receiving ecosystem are at least as important. In general, knowledge of the functioning of the receiving ecosystems is extremely limited. For example, interactions among the endemic roughly equivalent (to the target bivalve) species and its main competitors and predators, as well as its associated fauna and the rest of the ecosystem, are commonly lacking. Thus predictions of interactions of any new member of the community are necessarily based largely on studies from elsewhere and general ecological principles. Even when the information is available, novel interactions that could not be predicted are certain to arise, even with the best information and foresight. The case of *M. galloprovicialis* in South Africa is a good example. The intertidal ecology and biodiversity on the west coast of the country, where *M. galloprovicialis* is spreading (McQuaid and Phillips 2000), are both very well studied and understood (Branch and Steffani 2004). The area is characterized by a high biomass and relatively low species diversity (Bustamante and Branch 1996) and intense upwellings create strong gradients in productivity along the coast (Bustamante et al. 1995). Consequently, Branch and Steffani (2004) were able to predict fairly well the spread and effect of the introduction of *M. galloprovicialis* at a variety of levels of complexity of the ecosystem. However, they had no way of predicting that the establishment of *M. galloprovicialis* would lead to massive die-offs of *Ovalipes trimaculatis*, a mobile burying predatory crab in the surf zone of sandy beaches. Apparently *M. galloprovicialis* spat settle on the eyestocks and mouthparts of the crab, which are the only hard substrate in that particular ecotype, effectively killing the animal. Some interactions simply cannot be predicted and any introduction will have some unforeseen effects.

The effects of hitchhiking species are even more complex as most are typically poorly studied and thus their role in any new environment is even harder to predict. To use a recurring example, the suite of tunicates in Prince Edward Island seems to have become a fairly unassuming part of the ecosystem in the central part of the New England states (see above). However, they are not so limited in their influence in PEI. The possible reasons for this may include eutrophication or other sources of disturbance in PEI embayments, many of which are hyper-eutrophic because of catchment basin land-use patterns (Meeruwig et al. 1998; Meeruwig 2002; Raymond et al. 2002). There has also been the suggestion that another invasive species, the green crab, may be facilitating their time there (Locke et al. 2005). A number of authors have suggested a link between disturbance in the form of eutrophication and the susceptibility of a system to invasion by exotic species (Ruiz et al. 1999; Ruiz et al. 2000) Indeed, invasive species have been found to out-compete native species or fill vacant niches (see Herbold and Moyle 1986) under such conditions. Examples may be found for macrophytes (Bertness et al. 2002), algae (Wikström and Kautsky 2004), phytoplankton (Smayda and Reynolds 2001) and invertebrates (Currie et al. 2000). These factors interact in myriad ways to modify ecosystem processes and communities. However, most of these interactions are only theoretical and are little studied (Cloern 2001). Whatever the cause, the fact that they are invasive in PEI but not just south of there underlies the point that prediction of impacts may not be made simply by comparing similar situations.

Quarantine, disinfection and other protocols to limit risk

To prevent the spread of the target bivalves, a number of ideas have been put forward and discussed (Shatkin et al. 1997; Anonymous 2004). The simplest one has been to select species that cannot complete its lifecycle in the receiving environment so that the industry will be dependent upon hatcheries. Although this approach has a certain simple appeal, such a species may also not be particularly well adapted for the grow-out environment in other ways and thus will probably not be the optimal species for the industry. The idea that a target species may be limited to a small geographical area because of particular environmental conditions also has problems. First, if it may thrive and reproduce there, then other vectors (Ruiz and Carlton 2003) become important and secondary spread outside of the original point of introduction is likely (Anonymous 2004). More intrusive methods, including polyploidy and genetic modification to produce essentially sterile individuals, have also been suggested. Although polyploidy is feasible in a hatchery situation, all individuals are not affected (Shatkin et al. 1997) and thus spread is possible.

If introduction is deemed acceptable, as outlined above, one of the first lines of defence to limit the effect of exotic species with aquaculture practices should be to establish quarantine and/or disinfection protocols. The first choice for introductions should be to use hatchery-raised and tested stock grown in "clean" areas (Minchin and Rosenthal 2002). However, this is not always feasible in day-to-day operations of bivalve culture sites as stock is often relayed among sites at a regional scale. Thus, treatments must be done to limit the risk of transferring hitchhikers along with the stock.

Using the suite of tunicates described above for Prince Edward Island as an example, a number of treatments have been evaluated around the world, including dipping the mussel lines and equipment used in the culture operations in or spraying on acetic acid, brine or lime solutions, fresh water, drying, heat, etc. (Boothroyd et al. 2002; Anonymous 2003; Bourque et al. 2003a; Carver et al. 2003; Forrest et al. 2004; Mineur et al. 2004; Thompson and MacNair 2004; MacDonald et al. 2005; Swan et al. 2005). To date, different producers employ different management strategies with lesser or greater success. Other methods have also been tried for other species elsewhere with varying success. For example, Mineur (2004) examined the efficacy of using pressure washing to clean oysters in an experiment that simulated "normal" operational culture conditions. After washing, the oysters were then incubated for 40 days under laboratory conditions with a clean water source, following which time about 20 species of algae were observed to be growing on the oyster shells, including a few invasive species found only in that culture site so far. Minchin and Rosenthal (2002) discuss how a shipment of *C. gigas* from Japan to France led to the introduction of a number of species into Europe, despite the fact that upon arriving in France, the oysters were subjected to a brine dip to kill the organisms attached to the shell. They (Minchin and Rosenthal 2002) temper this observation by suggesting that the invaders may have been within the mantle cavities or tissues of live oysters or within the shells of dead ones. However, Shatkin (1997) outlines how similar transfers from Japan and British Columbia to France that had been treated with freshwater baths and inspected led to the establishment of a number of species, including barnacles and algae that were stuck to the outside of the oysters. In short, disinfection of bivalves for external hitchhikers is not always that successful.

The use of dips, etc., does not address the problem of introducing organisms that live within living bivalves or the shells of dead ones and thus most parasites, bacteria, viruses, and protozoan diseases as well as some phytoplankton will not be addressed using these methods (Minchin 1996). The alternative here is to use depuration so that the target bivalves can clear themselves of the organisms of concern. Although long-used to purge bivalves of toxins associated with, among various factors, toxic phytoplankton and for coliforms and other noxious human-associated microbes (Otwell et al. 1991; Sekiguchi et al. 2001; Blanco et al. 2002; Lee and Younger 2002), such an approach has also been shown possible for toxic phytoplankton themselves (Scarratt et al. 1993; Dijkema 1995, cited in Kaiser and Beadman 2002). However, efficacy is both bivalve- and phytoplankton species-dependent (Hégaret et al. 2006). Similarly, recent work by Bushek et al. (2004) has also shown that depuration or quarantine of shucked oyster shells prior to use as oyster cultch is important to limit the potential spread of the protozoan parasite *Perkinsus marinus* among regions. Depuration will not however work for organisms that are not released by bivalves over time. This includes many parasites, bacteria, and other bivalve-related pathogens. In these instances, quarantine and growth of F1 individuals for introduction is prescribed (Minchin and Rosenthal 2002). This approach is also, however, ineffective for vertically transmitted pathogens. Barber (1996) gives an example of how a protozoan parasite, *Perkinsus karlssoni*, persisted for 10 generations in quarantined *A. irradians* populations in Prince Edward Island. Further, any monitoring to see if stock is "clean" is only as good as the test used for monitoring and hitherto unknown species that may only be expressed once in a new environment cannot be detected (Minchin 1996).

The efficacy of the above protocols to limit risk is obviously a function of how well any guidelines are followed. As pointed out by Minchin and Rosenthal (2002), unauthorized transfers and introductions of bivalves is a serious issue that poses a risk to future bivalve production and ecosystem integrity. They (Minchin and Rosenthal 2002) give an international (USA to Ireland) example but the same issues exist at regional scales where bivalves are transported among sites for grow-out or relaying (Wasson et al. 2001).

KNOWLEDGE GAPS AND RECOMMENDED RESEARCH

- Preliminary risk analyses, as outlined in the section on management issues, should be done to identify knowledge gaps with respect to exotic species in bivalve culture (the cultured bivalves themselves and hitchhiking species).
- Directed research should be used to address these knowledge gaps prior to the introduction of bivalves into a system for aquaculture.
- Obtain baseline information on the receiving environment (physical and biological) to make predictions with respect to exotics and to evaluate and understand their influence.
- Predict the ability of exotics to establish and spread in the receiving environment.
- Predict the effect of exotic species on receiving ecosystems, including interactions with local species, habitat modifications, energy flow, etc.
- More information is needed on the requirements and influence of hitchhiking species in the environment. This is particularly true for a number of currently problematic species (e.g., tunicates).
- More information is needed with respect to the natural history of most exotic species.
- More information is needed with respect to the relative importance of natural (currents, dispersion rates, etc.) and anthropogenic (stock transfers, processing, hull fouling, etc.) spread of exotic species.
- Remedial measures need be developed to mitigate effects and minimize spread.
- Research is needed to understand the links between the presence of exotic species and other stressors in the environment (e.g., eutrophication, climate change, fishing activities, contamination, etc.).

GENETIC INTERACTIONS BETWEEN CULTURED AND WILD BIVALVES

The genetic effects of aquaculture activities on native populations are very difficult to assess and there is considerable disagreement regarding the consequence of genetic interactions between farmed and wild populations (Bentsen 1991; Saunders 1991; Gaffney and Allen Jr. 1992; Stotz 2000, Arnold et al. 2004). Potential intra-specific genetic interactions between wild and cultured populations are usually associated with large-scale salmonid farming, as presented by Peterson (1999), where the effects of genetic intrusion of escaped farm fish on wild salmon stocks are discussed in context of risks management. Nevertheless, these are general problems and they must be considered for all species reared in aquaculture facilities.

Genetic variation of a species can be partitioned into variation within and among populations. Any factor that reduces the overall genetic variability may compromise the capacity of a species to adapt to environmental change, and may even compromise the long-term survival of that species (Allendorf and Leary 1986). If the genetic variation within a given population is reduced, the population will be less able to adapt to change. Loss of variation among populations will result in convergence of populations towards one type and a narrower range of options for the species. The potential for genetic effects from shellfish aquaculture on wild species could occur at two levels: first, as a result of the potential risks associated with inbreeding from culture-based production or a reliance on cultured juveniles for stock enhancement activities; and, second, resulting from risks associated with transfers of organisms from aquaculture facilities to different areas within the species range.

RISKS ASSOCIATED WITH CULTURE CONDITIONS

Genetic change that often occurs during culture conditions can potentially affect wild population genetics (Allendorf and Ryman 1987; Jorstad and Farestveit 1999, Arnold et al. 2004). The production cycle of bivalve culture can include one or two spawning events in the natural environment that could affect the genetic integrity of the wild populations, if the genetics of the cultured populations has been modified. This could lead to an effect in the genetic integrity of the wild populations. This can also occur from shellfish enhancement activities, such as seed collected from artificial collectors or seed produced by aquaculture facilities. Bivalve enhancement activities using juveniles produced in hatcheries or collected over natural beds are either released in the area of capture (no genetic effect) or transferred to other grow-out areas (potential for genetic effect). The effects of all these practices on genetic variability of populations are poorly understood.

The loss of genetic diversity in hatchery-raised animals through inbreeding, selective breeding, or domestication is well documented (Cross and King 1993; Skaala et al. 1990; Stahl 1983). Low number of adult animal implicated in reproductive events, sperm competition, high variability in fecundity, and early larval success can all reduce the genetic variation of progeny compared with that of broodstock (Gaffney and Allen 1992; Beaumont 2000a; Beaumont 2000b). Providing that wild populations are genetically adapted to their natural environments, the release of hatchery stock and the subsequent hybridization with indigenous populations could affect the fitness of these wild stocks by reducing their overall genetic variation (Skaala et al. 1990; Stahl 1983). Ford et al. (2002) observed an increase in disease mortality associated with hard clam, *Mercenaria mercenaria*, aquaculture operation and Arnold et al. (2004) provide clear evidence that culture of species can influence the genotype composition of naturally occurring congeneric populations in the vicinity of the culture operation. Another potential threat to genetic variability of wild stock can occur when farmed stocks are released on a large geographical scale, allowing locally adapted populations to converge towards a common gene pool. This has occurred in Chile where wild scallops now represent only 10% to 15% of the total stock (Stotz 2000).

Changes in genetic diversity can also occur from seed collection and other husbandry practices, such as mussel socking operations. Through heterozygosity evaluations, Tremblay et al. (1998) demonstrated that mussel spat collected from ropes were not genetically different from wild mussel spats, but a gradual decrease in genetic variability (heterozygosity) did occur in the first year after socking. In contrast, mussels in continuous socks retained the same genetic diversity throughout the two-year production cycle (Tremblay et al. 2001). Authors suggest that traditional sleeving may induce losses of more heterozygous individuals. These losses seem to result from fall-off of more active individuals (more heterozygotes) through mesh of the socks and that factors limiting early fall-off, as the cotton cloth used in continuous socks, preserve genetic variability in culture mussels. Wild mussel stocks in bays without mussel culture had greater genetic variation than did wild mussels in bays with mussel culture (Tremblay et al. 1998); however, the density of wild stock is smaller than that of cultured stocks (Bruno Myrand, MAPAQ, personal communication). In regions where the biomass of wild mussels is significant (e.g. Prince Edward Island), the heterozygosity of wild mussels sampled in cultured sites was similar to those collected in non-cultured bays (Tremblay and Landry, in preparation).

Presently, we are unaware of any studies demonstrating clearly the long-term implications of these genetic interactions, but both positive and negative outcomes are possible.

RISKS ASSOCIATED WITH TRANSFERS OF ORGANISMS

With the recent expansion of the aquaculture industry in Canada, the transfers of organisms have likely increased considerably, and for the most part, are undocumented. A prerequisite to assessing the genetic effect of transfers on natural populations is to develop an understanding how the genetic structure of a species may be affected (Ryman and Utter 1987). Induced directional genetic changes in life history characteristics, as well as changes in allelic frequencies, are more likely to occur in species where gene flow is reduced. It is, therefore, critical to understand the distribution of genetic variation within or among populations to successfully evaluate the risk associated with transfers.

This basic scientific information is not available for most bivalve species in Canada. There are divergent theories regarding the existence of discrete, genetically differentiated populations for the same bivalve species in the east and west coast of Canada. The first theory, panmixia, assumes that pelagic shellfish larvae favor large-scale dispersion, which results in a significant gene flow among populations, particularly when they are geographically close (Berger 1973). Recruitment to an area would depend to a large extent on larval drift from other areas. The 1–2 month duration of the pelagic larval stage would allow larvae sufficient time to travel large distances and would support the panmixia theory. No immediate or long-term genetic risks associated with the transfer of organisms would be anticipated. There is evidence of gene flow between blue mussels (*Mytilus edulis*) in the Magdalen Islands and Prince Edward Island (Tremblay and Landry, in preparation), suggesting panmixia. However, stock transfer of mussels in the Gulf of St. Lawrence (Dickie et al. 1984; Mallet et al. 1990; Myrand and Gaudreault 1995, Myrand et al. 2002) showed an effect of origin on mussel performance suggesting genetic differentiation between populations.

Panmixia appears not to be the common genetic structure of marine molluscs (Hedgecock 1986; Beaumont 2000b and references therein). Indeed, it has been argued that the distribution pattern of giant scallops, *Placopecten magellanicus*, are characteristic of self-sustaining aggregations (Sinclair et al. 1985). This interpretation is based on aggregations, capable of sustaining a fishery, which are widely separated geographically. Oceanographic characteristics in these areas may allow scallop larvae to maintain a distribution independent of the residual circulation. Furthermore, there is growing evidence that molluscs species with similar life cycles, characterized by having widespread larval dispersion (i.e. mussels, oyster, and clams), do not always have increased gene flow. Significant differentiation can take place even between populations that are close on a geographical scale (Beaumont 2000b and references therein).

KNOWLEDGE GAPS AND RESEARCH RECOMMENDATIONS

Research on the population structure of wild molluscs must be conducted to assess the potential genetic consequences of farm/wild stock interbreeding. These studies should be done before farmed stock exceeds that of wild stock, with priority given to blue mussels (*Mytilus edulis* and *Mytilus trossulus*), scallops (*Placopecten magellanicus* and *Chlamys islandica*), quahaugs (*Mercenaria mercenaria*), and the soft clam (*Mya arenaria*). In the Gulf of St. Lawrence, genetic studies of the American oyster (*Crassostrea virginica*) indicate populations affected by extensive human-assisted homogeneity with some notable exceptions (Vercaemer, B., person. comm.). Consequently, regional-level genetic comparisons are no longer a priority, although there is still interest on a Pan-American scale.

To test the hypothesis that shellfish form self-sustaining, genetically differentiated populations, genetic variability should be determined on a temporal basis. Temporal, genetic stability is very critical, but often neglected in genetic studies. On the other hand, if temporal variations are important, then genetic differences between sites are transient and could be modified for each generation with genetically different cohorts. The sites are not defined as genetic entities but are part of a genetic mosaic fluctuating in time, often referred to as "chaotic genetic peachiness" (Johnson and Black 1984). Such a temporal variability has been observed in a number of marine organisms including bivalves (David et al. 1997; Li and Hedgecock 1998).

Without basic genetic information for wild stock, the genetic effect of shellfish culture will be difficult to evaluate. The information would provide baseline data by which the evolution of genetic diversity of and effects on wild shellfish populations could be measured. If aquaculture selectively affects genetic structure, monitoring of wild populations near aquaculture sites is necessary to ensure the genetic diversity in sympatric wild populations of core species is maintained.

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